EVOLUTION, GENETICS AND EUGENICS

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EVOLUTION, GENETICS AND EUGENICS

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THIRD EDITION



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THIS VOLUME
IS AFFECTIONATELY DEDICATED
TO
MY MOTHER

PREFACE TO FIRST EDITION

This book has been prepared to meet a specific demand, long felt here and elsewhere for an account of the various phases of evolutionary biology condensed within the scope of one volume of moderate size The present writer has now for sixteen successive years presented in lecture form to large classes of students the subjects of evolution genetics and eugenics. Never have we been able to find a single book that would cover the required ground In fact it has been necessary to require or at least to recommend, as many as three books. It is believed that the present book will furnish adequate reading material for a major or a semester course in evolutionary biology Some supplementary reading may be necessary in case an instructor wishes to emphasize one or more phases of the subject but for a first course in the subject we believe that all of the essential reading material will be found within the text itself

An effort has been made to present the subject in the best pedagogical order After a general introduction a rather long chapter appears in which the whole history of the development of evolutionary science is outlined together with the names and contributions of the leading evolutionists Part II is a presentation of the evidences of organic evolution, beginning with the bodies of evidence most definite and direct and ending with the less definite and more controversial Part III deals with causo-mechanical theories of evolution with Darwinism as the central topic. Part IV concerns itself with genetics or modern experimental evolution and Part V with eugenics or genetics as applied to human improvement.

The book consists largely of excerpts some long and some short from both the older classical evolutionary writers and the modern writers Our aim has been to select the most significant or characteristic passages from each author In most cases this ideal has been attained, but it has sometimes happened that we have had to make our selection of material to meet a real need in the book and accordingly have selected from an author a passage he himself might not consider particularly characteristic of his work We have succeeded, nevertheless in welding together out of a collection of isolated chapters and passages what seems to us to be a close approach to a coherent unit Unification has been accomplished by the aid of editorial connecting passages introductory statements criticisms and summaries. In certain cases it became necessary, for a variety of reasons

for the editor to write short chapters on certain topics that were not presented in the available literature in sufficiently brief compass or in sufficiently non technical language

The one man textbook is only too often written to emphasize the author's pet theories and is likely to be unduly biased The present work is completely non partisan It consists of the writings of many authors and presents many diverse theories The student is left to balance the various views one against another and to form his own judgment.

It is very unfortunate but none the less true, that even in these scientific days, the subject of evolution has a bad name in many communities and in many educational institutions with religious affiliations The mistake is made of supposing that evolution and religion are diametrically opposed The present writer has been at some pains to make it clear that evolution and religion are strictly compatible We teachers of evolution in the colleges have no sinister designs upon the religious faith of our students

While this book is intended primarily for a college textbook we have also had in mind the general reader Apart from a few of the more technical details, the text seems to us very readable The language of the great classic writers—Darwin, Wallace, Romanes De Vries, Le Conte—is simple and lucid. Among recent biological books few are written so freshly and vividly as those of Professor J Arthur Thomson. The clearness and scientific accuracy of Conklin, Saleeby Guyer, Walter, Lull Osborn, the Coulters, Downing, Shull, Tayler, Popenoe, Johnson, and others, are familiar to American biologists

Scrupulous care has been taken to verify all passages quoted but it is hardly likely that in so large a mass of material, all errors shall have been avoided The author and the publishers would welcome as a favor any suggestions or corrections submitted by interested readers

A list of the books from which material has been quoted is given on pages 612, 613 To the authors and publishers of these books and monographs we wish herewith to tender our grateful acknowledgments for their generosity and co-operation. A considerable amount of material for which permission to reprint had been granted fails to appear in the present volume It is hoped to incorporate this material in an appendix to a later edition, or else to use it in the form of a small volume of supplementary readings.

H H N

August 15 1921

PREFACE TO SECOND EDITION

A book of this sort somewhat resembles a loose-leaf encyclopedia in that it subjects itself very readily to revision and rearrangement and thus may be kept abreast of the times When certain sections prove through actual class use to need revision or restatement or when new discoveries necessitate a change in conclusions, appropriate corrections may be made, new matter added, or whole chapters rewritten When various topics have shown themselves to be either logically or pedagogically in the wrong order, it is easy to rearrange chapters, for the latter are to a large degree independent When, finally, any new chapter of superior excellence appears in a new publication, it is usually possible through the courtesy of author and publisher to add it to the worthy collection of excerpts already gathered together

The writer has been fortunate in that reviewers and colleagues both in America and in Europe have offered many constructive criticisms of the book and suggestions for its improvement It is hoped that the present edition will adequately reflect this expert advice

The order of presentation of the evidences of evolution has been changed from one based on the degree of directness of the evidence to one based on the logical succession of topics and their interdependence The chapters on "The Mutation Theory" and 'The Inheritance of Acquired Characters" have been placed near the end of the book in order that they may be considered in the full light of our present knowledge of genetics The chapter on "Linkage and Crossing over" has been rewritten in a more elementary and circumstantial style in order to overcome, if possible, the difficulty that students have always encountered in understanding the somewhat condensed and technical account of Professor Castle The discussion of mutations has been modernized and considerably extended through the addition of an article written especially for this book by Professor R Ruggles Gates and of a paper by Professor H F Muller The section on eugenics has been strengthened by the addition of a lucid

chapter from Albert Edward Wiggam's book *The Fruit of the Family Tree*. The writer has introduced a considerable amount of new matter of his own which consists chiefly of relatively short introductory, connecting, explanatory, and summarizing statements that serve to cement the otherwise somewhat disconnected excerpts into a coherent whole. Because of the fact that so many of the writer's own contributions are scattered through the book, it is deemed wise to omit his name from all such chapters and passages, with the understanding that all matter not specifically credited to others is his own.

Excerpts from books commonly contain undefined technical terms that perplex the beginning student. This difficulty has been overcome through the addition of a full glossary defining nearly all of the biological terms used in the book.

Grateful acknowledgments for the use of new materials are here with given to the following authors and publishers: E. G. Conklin, R. R. Gates, S. J. Holmes, D. F. Jones, T. H. Morgan, H. F. Muller, G. H. Thayer, A. E. Wiggam, E. B. Wilson, The Bobbs-Merrill Company, Henry Holt and Company, The Macmillan Company, The Princeton University Press, The Williams and Wilkins Company.

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UNIVERSITY OF CHICAGO
April 6, 1925

PREFACE TO THIRD EDITION

The first edition of this book was avowedly a book of readings, a source book, consisting almost exclusively of extracts from leading writers on evolutionary topics The character of the book made it somewhat disjointed It was criticized for lack of unity of plan and was called by one critic a hodge podge In spite of these defects many teachers found the book valuable as a reading source to accompany lectures

In the second edition an attempt was made to unify the material by the addition of a considerable amount of editorial comment in the form of short introductory and transitional chapters This method of unification was, however not sufficiently radical The result was neither a source book nor an organized textbook Believing that what most teachers want is primarily a textbook and only secondarily a source book the author has attempted to make the book a text by reorganizing the previously less organized material and by taking out and putting into the Appendix chapters that break the continuity of treatment but are useful for collateral reading

Teachers using the book recommended that the historical account of evolution and the section on evidences of evolution be left substantially as they were but they suggested that the section on genetics be largely rewritten This has been done The plan followed is that of dealing with genetics as the study of the mechanism of evolution the main factors of which are (1) the persistence factor heredity, (2) the diversity factor sexual reproduction and Mendelian heredity (3) the change factor, mutation, (4) guiding factors, selection and possibly the Lamarckian factor and orthogenesis, and (5) the dividing factor isolation in the broad sense The part on eugenics has also been extensively revised and rewritten, and contains a good deal more factual material It is hoped that in its present form the book may more nearly meet the needs of college classes in evolutionary biology

It gives us pleasure to acknowledge gratefully the permission given us by The Macmillan Company to use figures 40, 41, 42, 43, 44, 45, and 51

H H NEWMAN

University of Chicago
January 16 1932

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CHAPTER I

INTRODUCTION

WHAT ORGANIC EVOLUTION IS—DEFINITIONS

The following selections are representative both of the older and of the newer attitudes of thinkers on the subject of organic evolution The earlier writers were greatly impressed with the sublimity of the idea and found it in full accord with their religious faith The later writers are less awed by the vastness of the process and hence adopt a more completely materialistic attitude It is not necessary, however, to discard one's religious beliefs in order to adopt a scientific attitude toward the problems of organic evolution[1] These points of view are well expressed in the following quotations

"The world has been evolved, not created, it has arisen little by little from a small beginning, and has increased through the activity of the elemental forces embodied in itself, and so has rather grown than suddenly come into being at an almighty word What a sublime idea of the infinite might of the great Architect! the Cause of all causes, the Father of all fathers, the *Ens entium!* For if we could compare the Infinite it would surely require a greater Infinite to cause the causes of effects than to produce the effects themselves

"All that happens in the world depends on the forces that prevail in it, and results according to law, but where these forces and their substratum, Matter, come from, we know not, and here we have room for faith "—Erasmus Darwin,[2] as interpreted by Weismann

"When I first came to the notion, of a succession of extinction of species, and creation of new ones, going on perpetually now, and through an indefinite period of the past, and to continue for ages to come, all in accommodation to the changes which must continue in the inanimate and habitable earth the idea struck me as the grandest which I had ever conceived so far as regards the attributes of the Presiding Mind "—From a letter of Sir Charles Lyell to Sir John Herschel, 1836

[1] See Joseph Le Conte, *Relation of Evolution to Materialism* Appendix.

[2] From R. S Lull, *Organic Evolution* (The Macmillan Company Reprinted by permission)

"It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have all been produced by laws acting around us These laws, taken in the largest sense, being Growth with Reproduction Inheritance which is almost implied by reproduction, Variability from the indirect and direct action of the condition of life, and from use and disuse a Ratio of Increase so high as to lead to a struggle for Life, and as a consequence to Natural Selection, entailing Divergence of Character and the Extinction of less improved forms Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving namely, the production of the higher animals, directly follows There is a grandeur in this view of life with its several powers, having been originally breathed by the Creator into a few forms or into one, and that, while this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved —Charles Darwin, *Origin of Species*, concluding paragraph

"Speaking broadly we find as a fact that transmutation of species through the geologic ages has been accompanied by increasing divergence of type, by the increased specialization of certain forms, and by the closer and closer adaptation to conditions of life on the part of the forms most highly specialized, the more perfect adaptation and the more elaborate specialization being associated with the greatest variety or variation in the environment Accepting for this process the name organic evolution, Herbert Spencer has deduced from it the general law, that as life endures generation after generation, its character, as shown in structure and function, undergoes constant differentiation and specialization. In this view, the transmutation of species is not merely an observed process, but a primitive necessity involved in the very organization of life itself "—D S Jordan and V L Kellogg, *Evolution and Animal Life* (1908), p 4

"The Doctrine of Evolution is a body of principles and facts concerning the present condition and past history of the living and lifeless things that make up the universe It teaches that natural processes

have gone on in the earlier ages of the world as they do to-day, and that natural forces have ordered the production of all things about which we know "—Henry Edward Crampton, *The Doctrine of Evolution* (1911), p 1

"Evolution is the gradual development from the simple unorganized condition of primal matter to the complex structure of the physical universe, and in like manner, from the beginning of organic life on the habitable planet, a gradual unfolding and branching out into all the varied forms of beings which constitute the animal and plant kingdoms The first is called Inorganic, the last Organic Evolution " —Richard Swann Lull *Organic Evolution* (1917), p 6

THE MODERN ATTITUDE AS TO THE TRUTH OF THE EVOLUTION DOCTRINE

"Among that public which, though educated and intelligent, is not yet professionally scientific, there has been of late a widespread belief that naturalists have become very doubtful as to the truth of the theory of evolution and are casting about for some more satisfactory substitute, which shall better explain the infinitely varied and manifold character of the organic world This belief is an altogether mistaken one for never before have the students of animals and plants been so nearly unanimous in their acceptance of the theory as they are to-day It is true that there are still some dissentient voices as there have been ever since the publication of Darwin s Origin of Species but the whole trend of scientific opinion is strongly in favor of the evolutionary hypothesis "—William Berryman Scott, *The Theory of Evolution*, p 1

' But the biological sciences were still slower [than the physical sciences] to come to their true position as dignified science Here was the last stronghold of the supernaturalist. Thrust out from the field of 'physical science it was in the phenomena of life that the last stand was made by those who claim that supernatural agency intervenes in nature in such a way as to modify the natural order of events When Darwin came to dislodge them from this their last intrenchment, there was a fight intense and bitter, but, like all attempts to stay the progress of human knowledge, this final struggle of the supernaturalists was foredoomed to failure The theory of evolution has taken its place beside the other great conceptions of natural relations, and largely through its establishment biology has become truly a science

with a large group of phenomena consistently arranged and properly classified The discussion which followed the publication of Darwin's Origin of Species lasted for nearly a generation, but it is now practically closed so far as any attempt to discredit evolution as a true scientific generalization is concerned Scientists are no longer questioning the fact of evolution they are busied rather with the attempt to further explore and more perfectly understand the operation of the factors that are at work to produce that development of animals and plants which we call organic evolution —Maynard M Metcalf, *An Outline of the Theory of Organic Evolution* (1911), pp xxii–xxiii

Biologists turned aside from general theories of evolution and their deductive application to special problems of descent, in order to take up objective experiments on variation and heredity for their own sake This was not due to any doubts concerning the reality of evolution or to any lack of interest in its problems It was a policy of masterly inactivity deliberately adopted for further discussions concerning the causes of evolution had clearly become futile until a more adequate and critical view of existing genetic phenomena had been attained —E B Wilson (address as president of the American Association for the Advancement of Science 1914)

"The theory of development as it was revived by Darwin nearly half a century ago is in its modern form prevailingly unhistorical True it has forced beneath its sceptre the methods of investigation of all the sciences which deal with the living world and to-day almost completely controls scientific thought And yet science does not sincerely rejoice in its conquests Only a few incorrigible and uncritically disposed optimists steadfastly proclaim what glorious progress we have made otherwise, in scientific as in lay circles, there prevails a widespread feeling of uncertainty and doubt Not as though the correctness of the principle of descent were seriously questioned rather does the conviction steadily grow that it is indispensable for the comprehension of living nature, indeed self evident —Gustav Steinmann (translated by W B Scott from *Die Abstammungslehre* [1908] pp 1–2)

The many converging lines of evidence point so clearly to the central fact of the origin of forms of life by an evolutionary process that we are compelled to accept this deduction, but as to almost all the essential features whether of cause or of mode, by which specific

diversity has become what we perceive it to be, we have to confess an ignorance nearly total "—William Bateson, *Problems of Genetics* (1913), p 248

'The demonstration of evolution as a universal law of living nature is the great intellectual achievement of the nineteenth century Evolution has outgrown the rank of a theory, for it has won a place in natural law beside Newton's law of gravitation, and in one sense holds a still higher rank, because evolution is the universal master while gravitation is among its many agents Nor is the law of evolution any longer to be associated with any single name, not even with that of Darwin, who was its greatest exponent It is natural that evolution and Darwinism should be closely connected in many minds, but we must keep clear the distinction that evolution is a law, while Darwinism is merely one of the several ways of interpreting the workings of this law

"In contrast to the unity of opinion on the law of evolution is the wide diversity of opinion on the *causes* of evolution In fact, the causes of the evolution of life are as mysterious as the law of evolution is certain Some contend that we already know the chief causes of evolution, others contend that we know little or nothing of them In this open court of conjecture, of hypothesis, of more or less heated controversy the names of Lamarck, of Darwin, of Weismann figure prominently as leaders of different schools of opinion while there are others, like myself, who for various reasons belong to no school, and are as agnostic about Lamarckism, as they are about Darwinism or Weismannism, or the more recent form of Darwinism, termed Mutation by De Vries

"In truth, from the period of the earlier stages of Greek thought man has been eager to discover some natural cause of evolution, and to abandon the idea of supernatural intervention in the order of nature Between the appearance of *The Origin of Species* in 1859, and the present time there have been great waves of faith in one explanation and then in another each of these waves of confidence has ended in disappointment, until finally we have reached a stage of very general scepticism Thus the long period of evolution experiment, and reasoning which began with the French natural philosopher, Buffon, one hundred and fifty years ago, ends in 1916 with the general feeling that our search for causes, far from being near completion, has only just begun

Our present state of opinion is this we know to some extent *how* plants and animals and man evolve we do not know *why* they evolve We know for example that there has existed a more or less complete chain of beings from monad to man, that the one-toed horse had a four toed ancestor that man has descended from an unknown ape-like form somewhere in the Tertiary We know not only those larger chains of descent, but many of the minute details of these transformations. We do not know their internal causes, for none of the explanations which have in turn been offered during the last hundred years satisfies the demands of observation, of experiment, of reason. It is best frankly to acknowledge that the chief causes of the orderly evolution of the germ are still entirely unknown, and that our search must take an entirely fresh start. —H. F Osborn, *The Origin and Evolution of Life* (Charles Scribner s Sons), 1918, pp viii–x.

WHAT ORGANIC EVOLUTION IS NOT

1 The evolution doctrine is not a creed to be accepted on faith as are religious faiths or creeds. It appeals entirely to the logical faculties, not to the spiritual, and is not to be accepted until proved.

2 It does not teach that man is a direct descendant of the apes and monkeys, but that both man and the modern apes and monkeys have been derived from some as yet unknown generalized primate ancestor possessing the common attributes of all three groups and lacking their specializations.

3 It is not synonymous with Darwinism, for the latter is merely one man's attempt to explain how evolution has occurred.

4. Contrary to a very widespread idea, evolution is by no means incompatible with religion. Witness the fact that the early Christian theologians, Augustine and Thomas Aquinas, were evolutionists and the majority of thoughtful theologians of all creeds are today in accord with the evolution idea, many of them even applying the principle to their studies of religion for religious ideas and ideals, like other human characters, have evolved from crude beginnings and are still undergoing processes of refinement.

5. The evolution idea is not degrading Quite the contrary; it is ennobling as is well brought out by the classic statement of Darwin on page 4 and by that of Lyell, on page 3

6. The evolution doctrine does not teach that man is the goal of all evolutionary process, but that man is merely the present end product of one particular series of evolutionary changes. The goal

of evolution in general is perfection of adaptation to the conditions of life as they happen to be at any particular time. Many a highly perfected creature has reached the goal of its evolutionary course only to perish because it was too highly perfected for a particular environment and could not withstand the hardships incident to radically changed world-conditions. Many evolutions therefore have been completed while others are still awaiting the opportunity to speed up toward a new goal.

7. Evolution is therefore not entirely a thing of the past. Obviously some species, including Man perhaps, are nearly at the end of their physical evolution, but there are always certain generalized plastic types awaiting the next great opportunity for adaptive specialization.

CHAPTER II

HISTORICAL ACCOUNT OF THE DEVELOPMENT OF THE EVOLUTION THEORY

The chief sources of material for the present chapters are Osborn's *From the Greeks to Darwin*[1] and Judd's *The Coming of Evolution*[2]

Professor Osborn studies the evolution of the evolution idea as a biologist would investigate the evolution of a group of species, using all of the available sources of evidence at his disposal. The fragments of ancient writing and the crude imaginings of early natural philosophers are the fossils of the evolution idea, many of them ancestors of modern principles fragments of ancient or discarded ideas that still persist, though irrelevant to modern thought, are the vestigial structures that proclaim kinship between the past and the present, parallelisms between the development of ideas in the minds of independent thinkers do not prove plagiarism, but indicate common descent from the same ancestral ideas

This whole history is an important chapter in the story of human evolution in general, for it deals with the evolution of a characteristic human faculty—that of appreciating the broad relations that exist between the past and the present This faculty has evolved as truly as has an organic system such as the nervous system, and is unquestionably closely bound up with the latter

The evolution theory is a vast fabric of interrelated and interdependent facts and principles The fabric has been gradually woven out of separate threads and now stands strong though flexible with strands reaching into all sciences and tending to unify all science

It was only after the lesser ideas came to be clearly apprehended that it was possible for the master minds of Lamarck and of Darwin to weave them together into a consistent fabric and to bring the facts together under the one great conception, that of organic evolution Classification was a science comparative anatomy had made much progress the principles of embryology were fairly well understood,

[1] H F Osborn *From the Greeks to Darwin* (The Macmillan Company 1908)

[2] John W Judd *The Coming of Evolution* (Cambridge University Press 1911)

much palaeontological discovery had been made, before it was found that the facts from these sources all pointed to one general principle, and only one, that master principle "organic evolution"

We shall now trace the development of the evolution idea from its inception among the Greeks to its present status, and shall first give a brief account of Greek evolution

EVOLUTION AMONG THE GREEKS

The early Greek thinkers were sea people. "Along the shores and in the waters of the blue Aegean," says Osborn, "teeming with what we now know to be the earliest and simplest forms of animals and plants, they founded their hypotheses as to the origin and succession of life The spirit of the Greeks was vigorous and hopeful Not pausing to test their theories by research they did not suffer the disappointments and delays which come from one's own efforts to wrest truths from Nature"

The Greeks were anticipators of Nature Their speculations out stripped the facts in fact were usually made with "eyes closed to the facts' Their theories were inextricably bound up with current mythology, were naive, vague, and, from our modern point of view, ridiculous, yet they contained many grains of truth and were the germs out of which grew the saner ideas of subsequent thinkers

Thales (624–548 B C) was the first of the Greeks to theorize about the origin of life 'He looked upon the great expanse of mother ocean and declared water to be the mother from which all things arose and out of which they exist' This idea anticipates the modern idea of the aquatic or marine origin of life, and also the present idea as to the indispensability of water in all vital processes

Anaximander (611–547 B C) has been called the prophet of Lamarck and of Darwin While his theories were highly mythical in character, he conceived the idea of a gradual evolution from a formless or chaotic condition to one of organic coherence. He saw vaguely the idea of *transformation of aquatic species into terrestrial*, even deriving man from aquatic fishlike men (mythical mermen) who were able to emerge from the water only after they had undergone the necessary changes required for land life This idea involves that of *adaptation*, one of the cornerstones of the modern evolutionary structure

Anaximenes (588–524 B C), a pupil of Anaximander, 'found in air the cause of all things Air, taking the form of soul imparts life, motion and thought to animals" It is questionable whether this is a

prophecy of the importance of oxygen and oxidation in vital processes Anaximenes also introduced the idea of abiogenesis (spontaneous generation of living substance), his idea being that animals and plants arose out of a *primordial terrestrial slime* wakened into life by the sun's heat. This primordial terrestrial slime is perhaps a prophecy of Oken's ' Urschleim ' or of protoplasm

Xenophanes (576–480 B C), probably another pupil of Anaximander, agreed with his master so far as to trace the origin of man back to the transition period between the fluid or water and solid or land stages of the development of the earth ' He was the first to recognize *fossils* as the remains of animals once alive, and to see in them proof that once the seas covered the entire surface of the earth.

Heraclitus (535 475 B C) the first of a group of physicists, was the great proponent of the philosophy of change He was imbued with the idea that all was motion that nothing was fixed ' Everything was perpetually transposed into new shapes ' Although Heraclitus did not apply his ideas to living creatures and their evolutions, his philosophy was influential in molding the ideas of his successors

Empedocles (495 435 B C) ' took a great stride beyond his predecessors, and may justly be called the father of the Evolution idea He believed in Abiogenesis or spontaneous generation, as the explanation of the origin of life but that Nature does not produce the lower and higher forms simultaneously or without an effort Plant life comes first, and animal life developed only after a long series of trials ' He thought that all creatures arose through the fortuitous combination of scattered and miscellaneous parts which were attracted or epelled by the forces of love or hate (the two great forces in Nature) Thus arose every sort of combination of parts, some more or less harmonious and complete, others with ill assorted organization, lacking in some parts, double or triple in others Some of these combinations could not survive, because of their incompleteness and incongruity, but ' other forms arose which were able to support themselves and multiply ' This is a sort of vague prophecy of the survival of the fittest or of natural selection Four sparks of truth may be found in Empedocles' philosophy, ' first, that the development of life was a gradual process, second, that plants were evolved before animals third, that imperfect forms were gradually replaced (not succeeded) by perfect forms, fourth, that the natural cause of the production of perfect forms was the extinction of the imperfect '

Democritus (b 450 B C) said to have been the first comparative anatomist contributed to the substructure of evolution the idea of the adaptation of single structures and organs to certain purposes

Anaxagoras (500–428 B C) was the first of the Greeks to attribute the adaptations of Nature to Intelligent Design and was thus the founder of Teleology an idea that has played a retarding funct on in the history of evolution

With *Aristotle* (384 322 B C) we enter a new world says Osborn He towered above his predecessors and by the force of his genius created Natural History The evolution idea took a great step forward with Aristotle and reached a stage beyond which it did not go for many centuries He covered nearly the whole field touching upon most of the foundation stones of the complex problem His ideas like those of all the Greeks were often vague and in the light of present knowledge ncoherent but cons dering the meager factual background with which he had to work he had a surprising grasp of the whole situation Some of his princ pal ideas were

1 He had a clear idea of laws of Nature (Necessity) and attributed all evolutionary changes to natural causes

2 He opposed the ideas of Empedocles as to the fortuitous origin of adaptive characters and favored the idea of intelligent design in nature He was therefore a teleologist

3 Hence he rejected the hypothesis of the survival of the fittest because it was based on chance

4 He had substantially the modern conception of the Evolution of life from a primordial soft mass of living matter

5 He had an idea of a linear phylogenetic series beginn ng with plants then plant-animals such as sponges and sea anemones then animals with sensibility and thence by graded stages up to Man

6 He perceived the unity of type in certain classes of animals and cons dered rudimentary organs as tokens whereby Nature sustains this unity

7 He antic pated Harvey s doctrine of Epigenesis in embryonic development

8 He fully perceived the forces of hered tary transmiss on of the prepotency of one parent or stock and of Atav sm and Reversion

9 He is the father of that ancient fallacy called prenatal influ ences and believed in the inheritance of acquired characters as is shown in the following passage

"Children resemble their parents not only in congenital characters, but in those acquired later in life For cases are known where parents have been marked by scars and children have shown traces of these scars at the same points a case is also reported from Chalcedon in which a father had been branded with a letter and the same letter somewhat blurred and not sharply defined appeared upon the arm of the child "

POST-ARISTOTELIANS

With Aristotle the evolution idea reached a high watermark and thereafter the tide steadily declined Pliny Epicurus, Lucretius, and others kept the idea alive, but added nothing of importance to Aristotle s contribution

Lucretius (99–55 B C) appears to have been chiefly a follower of Empedocles in so far as his ideas as to the origin of animals are concerned He ignored Aristotle and his much more advanced philosophy of Nature finding the earlier, more mythical conceptions better suited to poetic expression He was not truly an evolutionist for he believed that all animals and plants arose fully formed from the earth Lucretius is of importance chiefly as a retarding factor, for his ideas were accepted and admired even up to the eighteenth century, witness Milton s immortal verse

> "The Earth obey'd, and straight,
> Op'ning her fertile womb, teem'd at a birth
> Innumerous living creatures, perfect forms,
> Limb'd and full grown "

THE EARLY THEOLOGIANS

The evolution idea made no progress from the time of Aristotle until the revival of learning in the Middle Ages The chief inhibiting factor was the church, which favored traditional knowledge and the special-creation idea in its most literal form Yet the early theologians, such as Gregory, Augustine, and Thomas Aquinas, were open-minded about the evolution idea and attempted to reconcile it with the scriptural account of creation

"*Gregory of Nyssa* (331–396 A D) taught," says Osborn, "that Creation was potential God imparted to matter its fundamental properties and laws The objects and completed forms of the Universe developed gradually out of chaotic material !"

Augustine (353–430 A D) conceived the idea, now so generally adopted by theologians, that the biblical account of creation is allegorical "In explaining the passage 'In the beginning God created heaven and the earth,' he says

"In the beginning God made the heaven and the earth, as if this were the *seed* of the heaven and the earth, although as yet all the matter of heaven and of earth was in confusion, but because it was certain that from this the heaven and the earth would be, therefore the material itself is called by that name "

Thomas Aquinas (1225–74), who wrote much later and was one of the leading church authorities, satisfied himself with merely expounding Augustine "As to the production of plants, Augustine holds a different view, for some say that on the third day plants were actually produced, each in its kind—a view favoured by the superficial reading of Scripture But Augustine says that the earth is then said to have brought forth grass and trees *causaliter*, that is, it then received the power to produce them For in those first days God made creation primarily or *causaliter*, and then rested from His work."

THE REVIVAL OF SCIENCE

During the long centuries until the awakening of science in the Middle Ages the evolution idea smouldered along in the minds of a few thinkers, but it was only when a few daring spirits broke the trammels of scholasticism and began once more to give free rein to observation and speculation that the idea once more burst into flame and began its second great period of advance

A small group of natural philosophers, scarcely more scientific in their methods than the Greeks, were the first to revive interest in the evolution idea Of these the names of Bacon, Descartes, Leibnitz and Kant are the most famous

Francis Bacon (1561–1626) did much to revive the vogue of Aristotelian ideas He also added some new ideas (1) that the mutability of species was the result of the accumulation of variations, (2) that variations of an extreme kind equivalent to ' mutations ' sometimes occur, (3) that new species might arise by a degenerative process from old species

Emmanuel Kant (1724–1804) was purely a philosopher, not an observing naturalist, but he profited by the writings of the contemporary naturalists especially those of Buffon and Maupertuis His

general ideas of evolution were comprehensive and summed up the best features of all preceding writers but he did not contribute any thing new to the pressing problem of the causes of evolution

Real progress was not to be made through further speculation What was most needed was facts and it was the task of the naturalists to furnish these The earliest of the eighteenth-century naturalists were still anticipators of Nature in that their theories outran their facts Of these the names of Bonnet and Oken are the best known

Bonnet (1720–93) was an evolutionist only in the sense that he believed that the adult organism is present in the egg and evolves from it by a process of unfolding or expansion He was a zoological observer of some note, however and made some of the most important contributions of his time to the general subject He believed ' that the globe had been the scene of great revolutions, and that the chaos described by Moses was the closing chapter of one of these, thus the Creation described in Genesis may be only a resurrection of animals previously existing " This theory admits of no progress and is scarcely worthy of the name evolution

Oken (1776–1851) is known chiefly for his "Urschleim" doctrine and his ideas of cells as vesicular units of life According to him, "Every organic thing has arisen out of slime and is nothing but slime in various forms This primitive slime originated in the sea from inorganic matter " These ideas are purely speculative, but suggest our modern ideas of protoplasm and cells

THE GREAT NATURALISTS OF THE EIGHTEENTH CENTURY

Three great names stand out above all the rest during this period those of Linnaeus, Buffon, and Erasmus Darwin

Linnaeus (1707–78) was the father of taxonomy He contributed facts rather than theories, he invented our present system of binomial nomenclature of both animals and plants, and a great many of his generic and specific names still persist Unfortunately he was an ardent advocate of the special-creation idea, holding that all of the true species were created as they are known today, except that new combinations may have arisen through hybridization or through degeneration His influence was great, but was reactionary and proved a serious hindrance to the progress of the evolution idea

Buffon (1707–88), born the same year as Linnaeus has been recognized as the father of the modern applied form of the evolution idea He attempted to explain particular cases on an evolutionary

basis. He lived at a time when it was dangerous to express views that might be interpreted as unorthodox, and this may account for the apparent lack of conviction in his own ideas, for he wavered between special creation and evolution. His chief contribution is the idea of the direct influence of the environment in the modification of the structure of animals and plants and the conservation of these modifications through heredity. This seems to imply that he believed in the inheritance of acquired characters. He expressed himself as believing that climate has had a direct effect in the production of various races of man, that new varieties of animals have been formed through human intervention (an idea implying artificial selection), that similar results are produced by geographic migration and through isolation. He expressed the view that there is a great struggle for existence among animals and plants to prevent overcrowding and to maintain the balance of Nature. This appears to be an anticipation of Malthus' ideas on population, which were so influential in shaping the theories of Charles Darwin and of Wallace.

While many of his ideas appear to be highly advanced for his time, his special applications are open to serious criticism. He reasons, for example, that the pig as it exists at present could not have been formed on any original complete and perfect plan, but seems to have been formed as a compound from other animals. It has useless parts which could hardly have been a part of a perfect plan as originally conceived. He thought that "the ass is a degenerate horse and the ape a degenerate man."

On the whole Buffon was not a strong advocate of evolution and his influence was far from being as important as some recent writers appear to believe.

Erasmus Darwin (1731–1802), grandfather of Charles Darwin, was a physician, a naturalist, and a minor poet. Undoubtedly he transmitted to his grandson his thoughtful habit and love of science and was influential in shaping his ideas on evolution. The elder Darwin's theories as to the causes of evolution closely paralleled those of Lamarck, his distinguished contemporary in France, but it is now very generally conceded that the ideas of the two men were independently derived from similar materials. Erasmus Darwin laid little emphasis on the direct action of the environment, which had been Buffon's main dependence, and dwelt on the internal origin of adaptive characters. "All animals," he said, "undergo transformations which are in part produced by their own exertions in response to

pleasures and pains, and many of these acquired forms or propensities are transmitted to their posterity" One could ask for no clearer statement of the idea that acquired characters are inherited

The fierceness of the struggle for existence was clearly recognized by Dr Darwin He considers that this struggle is beneficial to Nature as a whole because it checks the too rapid increase of life One step farther in the argument, and he would have arrived at the idea of the survival of the fittest, but he never took that step He agreed with the early Christian fathers in his belief that the powers of development were implanted within the first organisms by the Creator and that subsequent evolution of adaptive characters went on without further divine intervention The power of improvement rests within the creature s own organizations and is due to his own efforts The effects of these efforts, he believes, are transmitted to offspring so that there might be a cumulative effect throughout many generations of the results of effort

Erasmus Darwin was perhaps the first to express clearly the ideas that millions of years have been required for the processes of organic evolution and that all life arose from one primordial protoplasmic mass He writes as follows

' From thus meditating upon the minute portion of time in which many of the above changes have been produced, would it be too bold to imagine in the great length of time since the earth began to exist perhaps millions of ages before the commencement of the history of mankind, that all warm blooded animals have arisen from one living filament, which the first great Cause imbued with animality, with the power of acquiring new parts, attended with new propensities, directed by irritations, sensations, volitions, and associations, and thus possessing the faculty of continuing to improve by its own inherent activity, and of delivering down these improvements by generation to posterity, world without end?"

LAMARCK

Lamarck (1744–1829), the greatest of French evolutionists, is now looked upon as ' the founder of the complete modern Theory of Descent " Osborn considers him "the most prominent figure between Aristotle and Darwin One cannot compare his *Philosophie zoologique* with all previous and contemporary contributions to the evolution theory or learn the extraordinary difficulties under which he laboured, and that his work was put forth only a few years after he had turned

from Botany to Zoölogy, without gaining the greatest admiration for his genius No one has been more misunderstood, or judged with more partiality by over or under praise The stigma placed upon his writings by Cuvier, who greeted every fresh edition of his words as a nouvelle folie,' and the disdainful allusions to him by Charles Darwin (the only writer of whom Darwin ever spoke in this tone) long placed him in the light of a purely extravagant, speculative thinker Yet as a fresh instance of the certainty with which men of science finally obtain recognition, it is gratifying to note the admiration which has been accorded to him in Germany by Haeckel and others, by his countrymen, and by a large school of American and English writers of the present day, to note, further, that his theory was finally taken up and defended by Charles Darwin himself, and that it forms the very heart of the system of Herbert Spencer "

Lamarck's main theory of evolution was expressed by him in the form of his four "laws '

I Life by its proper forces, continually tends to increase the volume of every body which possesses it, and to increase the size of its parts up to a limit which brings it about.

II The production of a new organ in the animal body results from the supervention of a new want which continues to make itself felt, and a new movement which this want gives rise to and maintains

III. The development of organs and their powers of action are constantly in ratio to the employment of these organs

IV Everything which has been acquired, impressed upon or changed in the organization of individuals during the course of their life is preserved by generation and transmitted to new individuals which have descended from those which have undergone these changes

It is about the last ' law ' that the controversy rages, for it upholds the idea that *acquired characters are inherited*, now known as the ' Lamarckian doctrine '

A somewhat more specific statement of Lamarck's theory of evolution may be summed up in the following list of factors which he considered as playing an essential rôle in evolution

1 ' Favorable circumstances attending changes of environment, soil, food, temperature etc , supposed to act directly in the case of plants, indirectly in the case of animals and man "

2 "Needs, new physical wants or necessities induced by the changed conditions of life Lamarck believed that change of habits

may lead to the origination or modification of organs, that changes of function also modify or create new organs By changes of environment animals become subjected to new surroundings, involving new ways and means of living Thus, certain land birds driven by necessity to obtain their food in the water, gradually assumed characters adapting them for swimming wading, or for searching for food in the shallow water, as in the case of the long necked kinds '

3 "Use and disuse To use an organ is to develop it, not to use it is to eventually lose it The anterior limbs of birds became capable of sustained flight through use the hind limbs of whales are lost through disuse, etc '

4. "Competition Nature takes precautions not to overcrowd the earth The stronger and larger living things destroy the smaller and weaker The smaller multiply very rapidly, the larger slowly A physiological balance is maintained

5 "The transmission of acquired characters The advantages gained by every individual as the result of the structural changes resulting from use or disuse are handed down to its descendants who begin where the parent leaves off, and so are able to continue the progression or retrogression of the character "

6 "Cross-breeding If when any peculiarity of form or any defects whatsoever are acquired, the individuals in this case, always pairing, they will produce the same peculiarities, and if for successive generations confined to such unions a special distinct race will then be formed But perpetual crosses between individuals which have not the same peculiarities of form result in the disappearance of all the peculiarities acquired by the particular circumstances '"

7 "Isolation 'Were not man separated by distances of habitation, the mixtures resulting from crossing would obliterate the general characters which distinguish different nations' This thought is expressed in his account of the origin of men from apes, and is not applied to living things in general "

In addition to his theories as to the causes of evolution, Lamarck was the first to present the idea of the tree of life, or phylogenetic tree, as a mode of representing animal relationships All previous classifications had been based on the idea of a single linear phylogenetic series, each lower group being supposedly ancestral to a higher group, and all in a single chain

We may best sum up Lamarck's work and influence in the words of Osborn

"Lamarck, as a naturalist, exhibited exceptional powers of definition and description, while in his philosophical writings upon Evolution, his speculation far outran his observations, and his theory suffered from the absurd illustrations which he brought forward in support of it His critics spread the impression that he believed animals acquired new organs simply by wishing for them His really sound speculation in Zoology was also injured by his earlier thoroughly worthless speculation in Chemistry and other branches of science Another marked defect was, that Lamarck was completely carried away with the belief that his theory of the transmission of acquired characters was adequate to explain all the phenomena He did not like his contemporaries, Erasmus Darwin and Goethe perceive and point out, that certain problems in the origin of adaptations were still left wholly untouched and unsolved His arguments are, in most cases, not inductive, but deductive and are frequently found not to support his law but to postulate it

"It is now a question whether Lamarck s factor is a factor in Evolution at all! If it prove to be no factor, Lamarck will sink gradually into obscurity as one great figure in the history of opinion If it prove to be a real factor, he will rise into a more eminent position than he now holds,—into a rank not far below Darwin"

CUVIER AND GEOFFROY ST HILAIRE

Georges Cuvier (1769–1832) deserves especial mention as one of the strongest negative factors in the development of the evolution idea He was first of all an opponent of Lamarck, and, second of evolution in general He ranged himself with Linnaeus as a special creationist and advocated the idea of fixity of species ' All the beings, ' said he ' belonging to one of these forms (perpetual since the beginning of all things, that is the Creation) constitute what we call species " So able was Cuvier and so much in favor at the French court that he succeeded in throwing Lamarck s views into disrepute and thus greatly retarded the progress of evolution He was brilliant as a comparative anatomist and palaeontologist and will long be known for his discoveries in these fields

E Geoffroy St Hilaire (1772–1844) did his best to defeat the retarding influence of Cuvier The two engaged in a long and bitter controversy over the evolution idea While not a supporter of Lamarckism proper, he was a thoroughgoing evolutionist favoring

the doctrine of Buffon, that the direct action of the environment was the sole cause of evolution He also in a sense, anticipated De Vries, in that he believed that new species might be formed by transmutation or sudden large variations occurring in one generation "Hence the underlying causes of transformations he said, ' were profound changes induced in the egg by external influences, accidents as it were, regulated by law The controversy between Cuvier and St. Hilaire was a losing one for the latter The cards were stacked against him and after him the evolution idea was retired to comparative obscurity until revived by Charles Darwin

CATASTROPHISM AND UNIFORMITARIANISM

The development of the science of geology had a profound influence upon that of evolution The prevailing theories as to historical geology during the Middle Ages involved the idea of ' catastrophism According to this view all important changes in the earth's crust represented sudden radical transformations, involving earthquakes, volcanic outbursts, floods sudden upliftings of submerged areas, or equally sudden submergence of land bodies From these ideas naturally grew the related idea of great world wide destructions of animals and plants followed by re creation of new faunas and floras Cuvier, for example interpreted the more or less distinct fossil strata as being the result of a series of tremendous cataclysms, the last of which had been the great deluge of Scripture in which Noah figured prominently He thought that at each cataclysm great floods of water had covered the earth that the existing animals had been buried in mud and thus preserved as fossils, and that a new creation followed each cataclysm The great strength of this conception was that it appeared to give scientific support to both special creation and the Mosaic account of the ' Flood As compared with the pure evolutionary conception this alternative was highly acceptable to the church and was proclaimed as orthodox The Scotch philosopher and geologist, Hutton, who lived during the last half of the eighteenth century, combated the idea of catastrophism by advocating the doctrine of "uniformitarianism,' a view involving the idea that past changes on the earth were the result of the same sort of gradual changes as are observed to be taking place today—in brief, that there has been a strict uniformity of change throughout the entire period of geologic history There may have been, according to this view, local catastrophes,

such as volcanic outbursts, earthquakes and floods, but the main trend of change has been slow and constant, due largely to erosion and allied phenomena This view had practically no influence on the ideas of the time and for a long period the idea of catastrophism triumphed over the more truly evolutionary view of uniformitarianism, thus the evolution idea was destined to lie dormant till revived by Charles Darwin

THE REAWAKENING OF THE EVOLUTION IDEA

A number of important influences paved the way for the rehabilitation of the evolution idea at the hands of the younger Darwin Which of these was the most important it is difficult to say Probably Charles Lyell s *Principles of Geology* and Malthus *On Population* were the most suggestive works that Darwin encountered He was also doubtless influenced by Robert Chambers' *Vestiges of Natural History of Creation* which appeared in 1844

Charles Lyell (1797–1875) so successfully rehabilitated the doctrine of uniformitarianism in geology that it became very generally accepted, thus paving the way for a more favorable consideration of the idea of organic evolution Charles Darwin as a very young man took Lyell s *Principles of Geology* with him on his voyage on the ' Beagle and read it with the greatest devotion as is evidenced by his dedication of the journal of his voyage ' To Charles Lyell, Esq , F R S , this second edition is dedicated with grateful pleasure as an acknowledgment that the chief part of whatever scientific merit this Journal and other works of the author may possess has been derived from studying the well known, admirable *Principles of Geology*

Malthus influence on Darwin s ideas is well expressed by Judd as follows

' Fifteen months after this 'systematic inquiry began [referring to Darwin s exhaustive working over of his notes taken during his voyage on the 'Beagle] Darwin happened to read the celebrated work of Malthus *On Population* for amusement, and this served as a spark falling on a long prepared train of thought The idea that as animals and plants multiply in geometrical progression while the supplies of food and space to be occupied remain nearly constant, and that this must lead to a struggle for existence of the most desperate kind, was by no means new to Darwin, for the elder De Candolle, Lyell, and others had enlarged upon it yet the facts with regard to

the human race, so strikingly presented by Malthus, brought the whole question with such vividness before him that the idea of Natural Selection flashed upon Darwin s mind '

CHARLES DARWIN (1809–82)

Charles Darwin is without question the foremost figure in the development of the evolution idea and probably in the development of science in general The publication of his book, *The Origin of Species*, in 1859, was the most important event in biological history As has been already shown Darwin s chief ideas had been anticipated not by one but by several of his predecessors Nevertheless, he was the first to furnish a really adequate proof of the fact of evolution and his causo mechanical theory to explain the method of evolution was supported by a mass of systematically arranged data such as has been paralleled neither before nor since Darwin was the first evolutionist effectively to employ the inductive method, that of everywhere seeking facts first and then devising theories to fit the facts He never allowed speculation to outstrip observation, as nearly all of his predecessors had done, but made theory await the amassing of facts in its support, until the accumulation of the latter seemed almost to speak out the theory of themselves Our greatest debt to Darwin is due to his establishment of the factual basis of evolution, his selection theory was relatively of minor significance in so far as its value in the development of the evolution idea was concerned Yet this latter theory gained the widest acceptance among the scientifically inclined during the entire post Darwinian period It has been viciously assailed on all sides and has tottered repeatedly under the attacks of well trained adversaries Some of the weaker elements of the theory have given way under stress, and the whole selection factor as a primary causal factor in evolution has been seriously called into question, but since Darwin's time *the fact* of evolution has been almost universally accepted

The story of Darwin's life is almost a romance "Born in 1809," says Lull,[1] "this emancipator of human minds from the shackles of slavery to tradition saw the light of day upon the very day that ushered in the life of Abraham Lincoln, the emancipator of human bodies from a no more real physical bondage Darwin studied first at Edinburgh, but finding medicine unsuited to his tastes, entered Christ's College, Cambridge, as a candidate for the church His love

[1] Richard Swann Lull *Organic Evolution* (The Macmillan Company, 1917)

of Nature, however, dominated all other interests and shortly after graduation an opportunity came to join the ship 'Beagle' as naturalist in a voyage of exploration around the world The five years spent upon this memorable journey, the narrative of which is so admirably set forth in the book, *A Naturalist's Voyage around the World* resulted in the accumulation of the first of Darwin s great series of observations, the final decision to devote his life to zoological research and the beginning of that illness which made him a life-long invalid This last factor necessitated a retired life and thus proved of indirect benefit, as it enabled him to accomplish the immense amount of work which he did without being impeded by the distractions of a public career"

SUMMARY OF DARWIN S THEORIES

Since two subsequent chapters are to be devoted to Darwinism, only an outline of Darwin's theories need be presented in the present historical account

Although Darwin was an all round biologist and gave attention to practically every phase of evolutionary biology, he is known especially for his *selection theories* There are three of these the theory of artificial selection, the theory of natural selection, and the theory of sexual selection

a) *Artificial selection* —According to Darwin the commonest method of producing under human culture, new races of animals and plants is that of selection The breeder selects from among the highly variable individuals of a parent race those which possess the beginnings of desired modifications, and he breeds them together, expecting that the offspring will show the desired character, some in a more highly perfected condition others in a less The ones that vary favorably are again selected for breeding stock, and the same process is carried on until the desired character has been perfected

Although we now know that this is far from being a typical experience among breeders, it appeared to Darwin to be so typical that he transferred the selection idea from the breeder to Nature, making Nature the selecting agency responsible for the production of natural wild species His argument is as follows

b) *Natural selection* —The following factors are involved

1 All animals and plants tend to multiply in geometrical ratio

2 There is not food or room for a much larger number of animals and plants than now exist

3 All members of a species vary in many if not all directions

4 Those that vary in the more favorable directions, so as better to fit them to meet the conditions of life, survive in larger numbers than those varying in less favorable directions This is Spencer's "survival of the fittest"

5 The survivors of one generation become the parents of the next and, therefore, the more favorable characters are passed on more largely than the less favorable

6 There is in each generation a slow but definite approach toward complete adaptation to life conditions

7 Variations neither useful nor harmful would not be affected by natural selection and would be left either as fluctuating variations or as polymorphic characters

c) *Sexual selection* — This theory was offered to supplement that of natural selection, because Darwin considered the latter as inadequate to explain the facts of sexual dimorphism, or secondary sexual characters The theory is as follows There is always a contest among males for possession of females, in which the inferior males are eliminated either because they are, on the one hand, less courageous or weaker or less well equipped with weapons of combat, or because, on the other hand, the more attractive males, whether on account of colors, odors phosphorescence, behavior, etc., would succeed in winning mates from those less endowed Thus would be enhanced the sexual dimorphism until it reaches extremes in many cases that are truly remarkable

The name of *Alfred Russell Wallace* (1822–1913) will always be associated with that of Charles Darwin as co author of the theory of natural selection Wallace at the age of twenty-six went on a naturalistic expedition, primarily for collecting specimens from new regions He covered almost the same ground as did Darwin in his voyage on the "Beagle" Wallace had read Lyell's *Principles of Geology*, Malthus *On Population*, Chambers *Vestiges of Creation* While in Sarawak he tells us "I was quite alone with one Malay boy as cook, and during the evenings and wet days, I had nothing to do but to look over my books and ponder over the problem which was rarely absent from my thoughts" While thus engaged the idea of natural selection came to him as though by a sudden flash of insight When the idea was still in process of formation he wrote it out on thin paper and mailed it to Darwin, stating that he considered the idea new and asking Darwin to show it to Lyell, who had expressed interest in a

former paper of Wallace The ideas were expressed under the title *On the Tendency of Varieties to Depart Indefinitely from the Original Type*, and it proved to be an unusually concise and lucid statement of the main points of the natural selection theory Darwin at once wrote to Lyell as follows

"I never saw a more striking coincidence, if Wallace had my MS sketch, written in 1842, he could not have made a better short abstract! Even his terms now stand as heads of my chapters Please return to me the MS which he does not say he wishes me to publish but I shall, of course, at once write and offer to send it to any journal So all my originality, whatever it may amount to, will be smashed, though my book, if it ever have any value, will not be deteriorated, as all the labour consists in the application of the theory I hope you will approve of Wallace's sketch, that I may tell him what to say'

Lyell insisted that Darwin publish an abstract of his own work simultaneously with that of Wallace, and this course was carried out Darwin's generosity was equaled by that of Wallace who wrote, in 1870

"I have felt all my life and still feel the most sincere satisfaction that Mr Darwin had been at work long before me, and that it was not left for me to attempt to write *The Origin of Species* I have long since measured my own strength and know well that it would be quite unequal to the task"

Still later he wrote "I was then (and often since) the 'young man in a hurry,' he [Darwin] the painstaking student, seeking ever the full demonstration of the truth he had discovered, rather than to achieve immediate personal fame"

One must perforce admit the nobility of character of both men but there can be no serious competition between the two for the honor of being called the originator of the natural-selection theory

CONTEMPORARY OPINION REGARDING THE VALIDITY OF DARWIN'S VIEWS

At first Darwin was inclined to believe that the selection factor was all sufficient to account for the origin of species as well as that of adaptations, but as time passed he modified his earlier more sanguine views and came to the conclusion 'that natural selection has been the main but not the exclusive means of modification" Many of his followers went to such extremes in their advocacy of the all sufficiency of natural selection as would not have met with Darwin's approval

"The first effect of Darwin s works" says McFarland,[1] "was to carry the world of science by storm but at the same time to arouse intense hostility on the part of the theologians who found the theory of descent incompatible with the doctrines of Creation In this conflict Darwin took no part but was championed by Huxley, while Bishop Wilberforce led the opposition The battle was long and bitter there was much acrimonious writing on both sides but the theory of descent—the doctrine of evolution—was found to be invulnerable and at present the theologians themselves have accepted it and even make use of it in their own work

But as the years flew by the Darwinian doctrines began to meet with assaults from the scientists themselves who, having endeavored to prove their validity began to find them inadequate to the requirements of expanding knowledge The question was asked, 'What is the origin of the fittest? Given the fittest we easily understand how it is perpetuated but how does it arise? In the striking phrase of someone Natural selection might explain the *survival* of the fittest but fails to account for the *arrival* of the fittest!"

Darwin s main supporters during the most trying controversial period were Herbert Spencer and Thomas H Huxley

Herbert Spencer (1820–1903) was an extremely able supporter of the general theory of evolution, but was more definitely an advocate of Lamarckism than of natural selection His rôle was that of a champion of the whole philosophy of evolution as opposed to special creation and it was largely due to his forceful writings that Darwinism won the battle against dogmatism Spencer tried to explain the structure of protoplasm (living substance) on a physicochemical basis He thought of the structural units of protoplasm as comparable with the molecules of chemical compounds, each local region of the protoplasm in the organism being made up of different kinds of units which he called physiological units ' This conception of the physical basis of organic structure had a considerable influence in shaping Darwin s ideas and was probably the basis of the latter s provisional theory of pangenesis ' This theory was probably the first consistently worked out theory of the mechanics of heredity It was thought that every part of the body is continually giving off its particular kind of units (gemmules ') into the blood These gemmules are transported by the blood stream to all parts of the body and

[1] J McFarland, *Biology General and Medical* (The Macmillan Company, 1918)

collect in the germ cells This [illegible] that from the germ cell will devel[illegible] various details If a part of the [illegible] tioning or through changed en[illegible] gemmules, which, in turn, would [illegible] the modification to the next generat[illegible] factory even to Darwin and is now o[illegible]

Spencer is best known in the his[illegible] ardent neo-Lamarckian He states h[illegible] function produces change of structure [illegible] changes of structure so produced are inh[illegible] until it was cast down by Weismann.

Thomas Henry Huxley (1825–95), on[illegible] cal thinkers of the nineteenth century, [illegible] doctrine of evolution against Bishop Wil[illegible] an able investigator in the fields of compar[illegible] ology. "At the British Association at O[illegible] "after an American professor had ind[illegible] fortuitous concourse of atoms?' as a co[illegible] Dr Samuel Wilberforce, the Bishop of O[illegible] flippant attack on the *Origin* by enquiring [illegible] as Darwin's champion, if it 'was through his [illegible] mother that he claimed his descent from a [illegible]

"Huxley made the famous and well-de[illegible] and I repeat—that a man has no reason to [illegible] ape for his grandfather. If there were a[illegible] feel ashamed of recalling, it would rather [illegible] and versatile intellect—who not content wit[illegible] of activity, plunges into scientific question[illegible] acquaintance, only to obscure them by aim[illegible] the attention of his hearers from the real [illegible] digressions and skilled appeals to religious [illegible]

"Huxley himself accepted the theory o[illegible] not without some important reservations—[illegible] prevent him from becoming its most arden[illegible] Darwin used to acknowledge Huxley's gre[illegible] taking the defense of the theory—a defense [illegible] controversy and state of health made him [illegible] by laughingly calling him 'my general age[illegible] replying to the critics, declared he was 'Da[illegible]

Ernst Haeckel (1834–1919) was one of the earliest and most influential followers of Darwin in Germany In his *Generelle Morphologie*, published in 1866, seven years after the *Origin of Species* first appeared, he applied the doctrine of evolution, and especially the theory of natural selection, to the whole field of vertebrate morphology Beyond question Haeckel overapplied the theory and in a sense weakened its influence by his rather uncritical use of materials His writings have been translated into most languages and "are popularly believed to represent the best scientific thought on the matter" Biologists today however, are apt to look askance at Haeckel's works and to consider that they did more harm than good to Darwinism

August Weismann (1834–1914) was the first really original evolutionist after Darwin Like other thinkers of his time, he realized that further progress in the knowledge of the causal basis of evolution lay in further investigation of the causes of variation and the physical basis of heredity Weismann has been classed as a neo-Darwinian because he was a strong advocate of some form of selection, but his "selection" was not the selection of Darwin Realizing that the greatest weakness of the natural selection theory lay in its inadequacy as an originator of variations, he proposed the "germinal-selection" theory He contended that all heritable variations have their origin in the germ cell and therefore that a new type of organism arises only from a changed type of germ cell The germinal-selection theory stands out in striking contrast with Darwin's "pangenesis" theory The former is centrifugal, the latter centripetal "Determiners" of new characters, according to Weismann, arise in the germ plasm and work outward to all parts of the developing body, while the "gemmules," Darwin's equivalent of determiners, originate in the body tissues and are carried to the germ cells in each generation According to Weismann, there is a struggle among the determiners for the available food and favorable positions in the germ cell, and those that receive the most food and the best positions gain an initial advantage, so that they are able to initiate the development of larger or more perfectly adapted organs The descendants through cell division of these favored determiners are in a position to compete with other determiners on a more favorable footing in each succeeding generation so that the character represented by them steadily increases in a linear or definitely directed fashion until it reaches the state of complete adaptation or fitness Such a character may even continue its direct line of advance beyond the point of maximum fitness and result in

what are known as overspecializations The theory therefore would, if well founded, account not only for the initial stages of new adaptive characters, but also for overspecializations two phenomena that natural selection was unable to account for Not only were progressive evolutionary changes explained by germinal selection, but regressive changes seemed to be even more readily accounted for on this basis In the struggle among determiners in the germ cell some of the less favored units would be handicapped at the outset by insufficient food or unfavorable position and would produce smaller or less effective structures Progressively, from generation to generation, these weakened determiners would lose ground and become less and less successful in competition until they were weaklings among determiners and would be able to initiate only degenerate or vestigial structures or else would die out and lose their place altogether, thus accounting for total losses of structures

This theory does not exclude natural selection but rather increases its importance, for every structure that arises to the threshold of utility or disutility meets the winnowing process of natural selection The fitter individuals survive in the long run and these perpetuate the germ cells in which the successful determiners reside

A slightly different explanation of degenerating structures involves the principle of "panmixia" According to this idea changing environmental conditions may render certain adaptive organs of lessened value or of no value, as would be the case in the eyes of cave animals In different individuals the eye determiners would vary in their success in competition with other determiners, and since natural selection would no longer put a premium on perfect eyes, all grades of eyes would be equally inherited and gradually the poorer or degenerate eyes would become more numerous, till finally there would be no good eyes in the race Thus it will be seen that the germinal selection theory was auxiliary to natural selection and tended to support the latter at two of its weakest points But the supporting theory itself has the fundamental weakness of lacking a factual basis It is purely hypothetical and cannot be put to an experimental test Every time an objection to the theory was raised an auxiliary hypothesis was added to explain away the difficulty, till finally it fell to the ground through sheer top-heaviness, unable further to support its intricate structure of interrelated hypotheses

A much more valuable and lasting contribution of Weismann was his theory of "germinal continuity" and of the "apartness of the germ plasm" The whole theory has come to be known as the "germ plasm

theory," which forms the framework of nearly all of our modern genetics According to this view the germ plasm is immortal in that it is perpetuated from generation to generation through the instrumentality of mitotic cell division each germ cell being the product of the division of a previous germ cell back to the first germ cell that arose at the dawn of life Thus a germ cell cannot be a product of the soma but the soma is the product of germ cells The soma loses its generalized characters and specializes in various ways Once specialized soma cells are believed to have lost their capacity to play a germinal rôle Specialization means mortality Thus the relationship between parent and offspring is not that the parent gives rise to the offspring but that the same germ plasm gives rise to both parent and offspring

The logical conclusion to which this line of reasoning leads is that the changes in the soma no matter how produced, are helpless to produce any effect upon the germ plasm since germ cells come only from germ cells and not from soma cells Consequently Weismann led the assault against Lamarckism and won the day so conclusively that even in these modern times few biologists have the temerity to express aloud any definite belief in the inheritance of acquired characters Weismann's germ plasm idea is the cornerstone of modern genetics though there are some forward looking biologists who, looking at things with a physiological bias cannot make themselves believe in the total independence of any tissue—even the sacred germ plasm

Weismann's influence was very great especially during the last decade of the nineteenth century and his theories gave rise to an immense amount of research, chiefly of a cytological and embryological character

ISOLATION THEORIES

Among the theories subsidiary to natural selection as an aid to species forming are the various isolation theories One of the weaknesses inherent in natural selection had to do with the probable swamping out of new types by promiscuous breeding with the more numerous individuals of the older types "Anything says *Metcalf*, "which divides a species into groups which do not freely interbreed, is said to segregate (isolate) the members of the species into these subdivisions."

Some American writers, especially *Jordan* and *Kellogg*, *Gulick*, and *Crampton*, have dealt with the isolation factor in evolution and believe

that it is a major factor of as great importance in species forming, or nearly so, as natural selection But the prevailing opinion seems to be that isolation is really a kind of selection, more like artificial selection than anything else, which separates out certain pure lines and prevents promiscuous interbreeding Various agents are known to produce isolation by erecting barriers to interbreeding between groups of individuals within a species These segregative factors may be geographical, climatic, reproductive, physiological, or, in plants, the result of soil diversity Thus a mountain range, on the two sides of which a species migrates, effectively separates the species into two independent groups Heat, cold, moisture, etc., separate others. Reproductive incompatibility between new and older types is equally effective as is assortative mating of like with like Like natural selection, isolation has nothing to do with the origin of new types, but merely aids in the preservation of types when once formed Were there not spontaneous variations among animals and plants, there would be nothing to isolate Therefore isolation plays only an auxiliary rôle, helping to preserve new races once they are formed

ORTHOGENESIS THEORIES

'The orthogenetic evolution theories of various authors, based upon the assumed occurrence of variations in determinate lines or directions (a restricted and determinate variation as compared with the nearly infinite, fortuitous, and indeterminate variation assumed in the selection theories), are of several types The mention of two will reveal pretty well the more important characters of all Not a few biologists have always believed in the existence of a sort of mystic, special vitalistic force or principle by virtue of which determination and general progress in evolution is chiefly fixed Such a capacity, inherent in living matter seems to include at once possibility of progressive or truly evolutionary change Not all evolution is in a single direct line to be sure, ascent is not up a single ladder or along a single geological branch but these branches are few (as indeed we actually know them to be however the restriction may be brought about) and the evolution is always progressive, that is, toward what we, from an anthropocentric point of view are constrained to call higher and higher or more ideal life stages and conditions

'Other naturalists also seeming to see this source of determinate or orthogenetic evolution but not inclined to surrender their disbelief in vitalism, in forces over and beyond the familiar ones of the

physicochemical world have tried to adduce a definite causomechanical explanation of orthogenesis The best and most comprehensive types of this explanation are those essentially Lamarckian in principle in which the direct influence of environmental conditions the direct reactions of the life stuff to stimuli and influences from the world outside are the causal factors in such an explanation But while every naturalist will grant that such factors do change and control in a considerable degree the life of the individual most see no mechanism or means of extending this control directly to the species

The above-quoted paragraphs from Jordan and Kellogg[1] will serve to place before the reader the general ideas involved in the orthogenesis conception A brief account of the various special theories of orthogenesis follows

Carl von Nägeli s ideas of orthogenesis involve a belief in a sort of mystical principle of progressive development a something quite intangible that exists in organic nature which causes each organism to strive for or at least make for specialization or perfect adaptation This idea of an inner driving and directing force reminds one of the entelechy of Driesch or Bergson s creative evolution" Nageli believed that animals and plants would have developed essentially as they have without any struggle for existence or natural selection This form of orthogenesis theory then is alternative to natural selection

Theodore Eimer s theory of orthogenesis is more scientific and less mystical than Nageli s He believed that lines of evolution were not miscellaneous and haphazard, but were confined to a few definite directions determined at their initial stages not by natural selection but by the laws of organic growth aided by the inheritance of acquired characters A new character makes a beginning as would the first step in a slow chemical change or series of such changes, and it must go through to a fixed end under given conditions just as surely as does the chemical process Only when a given character or line of evolution results in the production of a very positive advantage or disadvantage to the species does natural selection step in to interfere with orthogenesis. The causes of orthogenesis are said to lie in the effects of external influences climate nutrition or the given constitution of the organism.

Actual species-forming or the breaking up into specific units of the orthogenetic lines of change depends according to Eimer, upon

[1] Jordan and Kellogg *Evolution and Animal Life* (D Appleton and Company)

three factors a standstill or cessation of development on the part of some lines, sudden development by leaps (practically mutations), and hindrance or difficulty of reproduction (the type of thing that Romanes emphasized as physiological isolation ten years later) Eimer illustrated his theories by the evolution of color patterns in lizards and those on the wings of butterflies In both he believed that longitudinal stripes were primitive, that rows of dots followed these which were in turn followed by crossbands, reticular patterns, and finally by solid coloration This hypothetical phylogenetic order is more or less closely paralleled by the ontogenetic order, in the lizards at least

It will be noted that Eimer's theory places natural selection in a subordinate position, but does not dismiss it altogether, as is done by Nageli It aids natural selection in explaining adaptations in that it furnishes for natural selection various characters of selective value, which may be either perpetuated or eliminated according to their utility

E D Cope, a leading American palaeontologist of the past century, had an orthogenetic theory involving his ideas of "bathmism" (growth force), "kinetogenesis" (direct effect of use and disuse and environmental influence), and "archaesthetism" (influence of primitive consciousness) It may be said that his ideas were Lamarckian throughout In common with the majority of palaeontologists of later date—Osborn, Williston, Hyatt, Smith, and others—Cope felt the need of some factor other than natural selection to explain the apparent steady progress of characters in definitely directed lines as seen in the fossils It is natural therefore that palaeontologists almost universally lay hold of both Lamarckian and orthogenesis ideas

Charles Otis Whitman, who until his death over twenty years ago was considered the leading American zoologist had strong leanings toward orthogenesis In one of his few publications he says

"Natural selection, orthogenesis, and mutation appear to present fundamental contradictions, but I believe that each stands for truth, and reconciliation is not far distant The so-called mutations of *Oenothera* are indubitable facts, but two leading questions remain to be answered First are these mutations now appearing, as is agreed, independently of variation, nevertheless the products of variations that took place at an earlier period in the history of these plants? Secondly, if species can spring into existence at a single leap, without the assistance of cumulative variations, may they not also originate with such

assistance? That variation does issue a new species and that natural selection is a factor, though not the only factor, in determining results, [illegible] though we cannot

genesis), and likewise of variations in various directions (amphigenesis) If I am not mistaken in this, the reconciliation for natural selection and orthogenesis is at hand'

In concluding this brief account of orthogenesis, it should be said that definitely directed evolution is now believed to be one of the laws of organic evolution but that we have no clear ideas as yet as to what are its underlying causes Therefore *orthogenesis is not a causo mechanical theory of evolution at all*

THE MUTATION THEORY OF DE VRIES

The theory of mutations is associated with the name of *Hugo De Vries*, the well known Dutch botanist that of 'heterogenesis with the name of *H Korchinsky*, a Russian

Though Korchinsky anticipated De Vries by several years, his work was not supported by the large amount of experimental data that characterized that of the great Dutch worker The relative claims for recognition as the founder of the mutation theory are almost on a par with those of Darwin and Wallace for the natural selection theory Both Darwin and De Vries held back their theories until they appeared to be adequately supported by personally collected facts

There is a striking parallelism between the ideas and conclusions of De Vries and those of Korchinsky, and since this is true a résumé of De Vries s better known work will serve to give the essentials of the whole conception

De Vries began his genetic experiments by a study of the variations of plants in the field After learning their normal variability in nature he transferred them to the experimental garden and there attempted to improve them by selection He found that the improved living conditions due to better soil and cultivation induced a wider range of variability in size, luxuriance, and fecundity Such variations were plus or minus in their character, fluctuating about a mean or average It was exactly this type of variability that Darwin emphasized as the raw material of evolution but De Vries found by experiment that selection had no permanent hereditary effect when based

to fluctuating variations, since the latter were merely somatic responses on variable growth conditions This negative finding led him to renewed interest in discontinuous or saltatory variations as the only alternative to fluctuating or continuous variations

He looked far and wide among species of wild plants for a species that might exhibit a significant amount of saltatory variation and finally discovered in the evening primrose (*Oenothera lamarckiana*) what seemed to exhibit exactly the hoped for characteristics. This large, stately plant with conspicuous yellow blooms had escaped from cultivation and was growing wild in the fields In addition to a large number of plants that showed only minor differences among themselves, De Vries found several individuals growing among the typical individuals which differed not merely in degree but in kind These were as different as distinct varieties, and, when the seeds were planted in the garden they bred true to their kind The only question now was whether they had actually arisen from typical parents To test this possibility, seeds of several typical plants were planted in the garden, the result being not only a repetition of the peculiar types observed in the field, but of about a dozen other true breeding types with well marked differences from the parent species and among themselves.

These new types De Vries considered as new elementary species and he called them "mutants" They came into existence suddenly in one generation and, as a rule, bred true Whatever factors were responsible for mutations, the seat of origin must have been in the germ cell and not in the soma Consequently they were inherited fully from the start The same mutations occurred in considerable numbers and in successive years In one case a given mutation occurred only once in eight years of observation Some mutants were robust and successful, others were weak and incapable of living under natural conditions, others were sterile On the basis of these results, which are reported in detail in chapter xxvi De Vries came to the conclusion that evolution was based upon the sudden appearance of new varieties or elementary species and not upon the natural selection of fluctuating variations.

The mutation theory compared and contrasted with the natural selection theory —It will be recalled that the raw material upon which natural selection works is the minute individual or continuous variation that is universal in all living forms and is known to be largely somatic in character and due to differences in environment. Darwin

did not distinguish between somatic and germinal variations The essential feature of mutations is that they are germinal in origin and therefore come forth full fledged in the first generation arising from the changed germ Darwin recognized "saltatory variations" or "sports,' which are mutations, but did not consider them of sufficiently frequent occurrence to furnish an adequate material for selection

De Vries, on his side, did not discard the principle of selection, but showed that selection acted as between mutants, serving to eliminate those which are unfit and allowing the sufficiently fit to survive alongside the parent types According to Darwin's view, the new types arose only at the expense of the old, for only through the elimination of the old (less fit) types could the new types progress toward further fitness Darwin's view was ill suited to explain the origin of new distinct types, because the process of selection proceeded by imperceptible steps De Vries s view gives us distinctly different, pure breeding types at once that, if isolated, would be new elementary species from the first

In conclusion it may be said that the mutation theory was at first intended as a substitute for natural selection, but that later the selection idea was adopted as a directive principle, guiding mutations toward adaptiveness

THE RISE AND VOGUE OF BIOMETRY

No historical account of the development of the evolution idea would be complete without a statement of the rôle played by biometry in the study of evolutionary data Biometry is the statistical study of variation and heredity During the last decade of the nineteenth century it became obvious to those who had followed the progress of the subject that farther advance toward the solution of the problem of the causes of evolution must come from a better understanding of variation and heredity, the two fundamental factors involved. Three main modes of attack were developed during these years the statistical (biometry), the experimental (chiefly breeding work), and the microscopical (cytology or the study of the minute structure of the germ cells)

Sir Francis Galton, a cousin of Charles Darwin, was the founder of biometry He applied certain already understood principles that had been developed mainly in the study of the laws of chance to the study of variations and, by comparing the boiled down formulas

resulting from his computations of parental generations with those of offspring, he arrived at two laws of heredity the law of filial regression, and that of ancestral shares of inheritance The essence of the first was that the offspring of exceptional parents tend to regress toward mediocrity in proportion to the degree of parental exceptionalness The second law was really explanatory of the first, for it was found that the offspring inherit not only from parents, but from the various grades of ancestors, and it was the pulldown of a miscellaneous ancestry that made for regression toward mediocrity It appeared that half of the hereditary influence could be assigned to parents, half of the remainder to grandparents, half of the remaining remainder to great grandparents, and so on down the line

Karl Pearson, a pupil and follower of Galton, has carried the study of biometry to a more highly refined state. His attempt has been to apply to the study of evolution the precise quantitative methods which are used in physics and in chemistry While much of Pearson's work is far beyond the range of the average professional biologist today, it is extremely useful as a tool in handling data in which great accuracy is demanded. Frequently, however, the methods are far too refined for the material, and much time is wasted in handling crude data by means of highly refined instruments of measurement and ultra accurate mathematical methods

On the whole the contributions of biometry to our understanding of the causes of evolution are rather disappointing About the only clean-cut finding has been the discovery that some variations are continuous and others discontinuous The former are capable of being expressed in a single curve with a single mode, while the latter are expressed in bimodal or polymodal curves. If material is homogeneous to start with it is likely to give monomodal curves, but if it is heterogeneous, its heterogeneity will be revealed by the plural modes In a subsequent connection (chapter xliii) some further account of the details of biometry will be presented We must for the present be content with having placed biometry in its setting as one step in the advance of the evolution idea

EXPERIMENTAL BREEDING

"While De Vries says Castle[1] "was engaged in his studies of the evening primrose he hit upon an idea far more important, as most biologists now believe, than the idea of mutation, though De Vries

[1] W E. Castle *Genetics and Eugenics* (Harvard University Press 1920) p 82

himself, both before and since, has seemed to regard it as of minor importance He called this the '*law of splitting of hybrids*' The same law, it is claimed was independently discovered about the same time by two other botanists, Correns in Germany, and Tschermak in Austria Further historical investigations made by De Vries showed that the same law had been discovered and clearly stated many years previously by an obscure naturalist of Brünn, Austria, named *Gregor Mendel* and we have now come to call this law by his name, *Mendel's Law* Mendel was so little known when his discovery was published that it attracted little attent on from scientists and was soon forgotten, only to be unearthed and duly honored years after the death of its author Had Mendel lived forty years later than he did, he would doubtless have been a devotee of biometry, for he had a mathematical type of mind and his discovery of a law of hybridization was due to the fact that he applied to his biological studies methods of numerical exactness which he had learned from algebra and physics In biology he was an amateur, being a teacher of the physical and natural sciences in a monastic school at Brunn Later he became head of the monastery and gave up scientific work, partly because of other duties, partly because of failing eyesight'

There had been plant hybridizers before Mendel, but their lack of exactness in technique had prevented them from discovering the law of segregation or splitting of hybrids

Joseph Gottlieb Kolreuter (1733–1806) who really belonged to the period of Lamarck, barely missed making the discovery that was afterward made by Mendel The salient features of his work are according to Castle[1]

"1 Kölreuter established the occurrence of sexual reproduction in plants by showing that hybrid offspring inherit equally from the pollen plant and the seed plant

"2 He showed that hybrids are commonly intermediate between their parents in nearly all characters observed, such for example as size and shape of parts

"3 Many hybrids are partially or wholly sterile, especially when the parents are very dissimilar (belong to widely distinct species) Such hybrids often exceed either parent in size and vigor of growth

"4 Kölreuter did not observe the regular splitting of hybrids which Mendel and De Vries record, but some of his successors did, particularly Thomas Knight (1799) and John Goss (1822) in England,

[1] *Op cit.*, p 86.

who were engaged in crossing the garden peas with a view to producing more vigorous and productive varieties, and Naudin (1862) in France, who made a comprehensive survey of the facts of hybridization in plants and came very near to expressing the generalization which Mendel reached four years later"

MENDEL'S LAWS

"The earliest experimental investigations of heredity," says Locy[1] in a concise summary of Mendel's work, "were conducted with plants, and the first epoch making results were those of Gregor Mendel (1822–1884), a monk and later abbot, of an Augustinian monastery at Brünn, Austria In the garden of the monastery, for eight years before publishing his results, he made experiments on the inheritance of individual (or unit) characters in twenty two varieties of garden peas Selecting certain constant and obvious characters as color, and form of seed, length of stem, etc., he proceeded to cross these pure races, thus producing hybrids, and thereafter, to observe the results of self fertilization among the hybrids

"The hybrids were produced by removing the unripe stamens of certain flowers and later fertilizing them by ripe pollen from another pure breed having a contrasting character The results showed that only one of a pair of unit characters appeared in the hybrid of the next generation, while the other contrasting character lay dormant Thus in crossing a yellow seeded with a green seeded pea, the hybrid generation showed only yellow seeds The character thus impressing itself on the entire progeny was called *dominant*, while the other that was held in abeyance was designated *recessive*

"That the recessive color was not blotted out was clearly demonstrated by allowing the hybrid generation to develop by self fertilization Under these circumstances a most interesting result was attained The filial generation, derived by self fertilization among the hybrids produced plants with yellow and green seeds, but in the ratio of three yellow to one green All green seeded individuals and one-third of the yellow proved to breed true, while the remaining two thirds of the yellow seeded plants, when self fertilized produced yellow and green seeds in the ratio of three to one

"*Subsequent breedings gave an unending series of results similar* to those obtained with the first filial generation.

[1] William A Locy *The Main Currents of Zoölogy* (Henry Holt & Company 1918), pp 37–39

"This great principle of alternative inheritance was exhibited throughout the extensive experiments of Mendel, and it is now recognized as one of the great biological discoveries of the nineteenth century

The essential feature of Mendel s discovery was not the phenomenon of dominance for relatively few instances of pure dominance have been discovered but *it was the phenomenon of segregation.* By segregation is meant that although determiners for opposed hereditary characters derived from diverse parental sources may unite in a common germ plasm for one generation they segregate out pure, or unmodified by their association together in the next and subsequent generations This law of segregation depends on the idea that the germ cell is composed of bundles of separately inheritable unit characters, which may be paired or grouped shuffled and redealt like cards, so as to give an infinite number of permutations and combinations without affecting the unit determiners themselves

From the evolutionary standpoint it is supposed that new unit characters arise by mutations and are fully hereditary They cannot be swamped out by interbreeding unless they are recessive, for they will dominate the old characters Even recessive characters could be perpetuated by segregation or by the union of two individuals possessing the determiner in the recessive condition as well as the dominant Thus a knowledge of the behavior of unit characters in heredity reveals part of the mechanism for conserving new characters if they are advantageous or even sufficiently fit to survive

New types or species might arise through processes of hybridization and the survival of individuals possessing the most favorable combinations of characters

"Evolution from this point of view," says Morgan,[1] "has consisted largely in introducing (by mutations) new factors that influence characters already present in the animal or plant

' Such a view gives us a somewhat different picture of evolution from the old idea of a ferocious struggle between the individuals of a species with the survival of the fittest and the annihilation of the less fit Evolution assumes a more peaceful aspect New advantageous characters survive by incorporating themselves into the race, improving it and opening to it new opportunities In other words the emphasis may be placed less on the competition between the indi

[1] T H Morgan *A Critique of the Theory of Evolution* (Princeton University Press, 1916) pp 87 88

viduals of a species (because the destruction of the less fit does not *in itself* lead to anything that is new) than on the appearance of new characters and modifications of old characters that become incorporated in the species, for on these depends the evolution of the race"

HYBRIDIZATION AND THE ORIGIN OF SPECIES

As a consequence of the great interest aroused by Mendel's hybridization experiments the question has arisen as to the rôle of hybridization in organic evolution Certain it is that a vast number of animal and plant races now existing are mixed or hybrid in nature and are continually splitting up into various Mendelian segregates How many pure races are there today? Some authors think that no variable races today are pure *Lotsy* goes so far as to claim and attempt to prove that unit characters are fixed and that the only source of variation is hybridization, or amphimixis Biologists today would not be willing to go thus far with *Lotsy*, but it seems beyond question that hybridization has played an important rôle in the production of very many groups now living It is of interest to recall that Linnaeus, though a special creationist, admitted the possibility of the origin of new species by hybridization

NEO-MENDELIAN DEVELOPMENTS

Since the rediscovery of Mendel s paper by De Vries and its perusal by thousands of biologists the world over, Mendelian breeding experiments with all manner of animals and plants has been the ruling passion of geneticists Among the leading neo Mendelians are Bateson, Morgan, Castle, Correns, East, Hurst, Shull, Tschermak, and the pupils of these

Perhaps the first two mentioned, Bateson and Morgan, have contributed most largely to an understanding of the intricacies of the Mendelian operations *Bateson* has become so imbued with the idea that all mutations are the result of the loss of factors that he proposes the hypothesis that "evolution has taken place through the steady loss of inhibiting factors," as Morgan puts it "Living matter was stopped down, so to speak, at the beginning of the world As the stops are lost, new things emerge Living matter has changed only in that it becomes simpler" It is quite probable that Bateson, in proposing so radical a view, intended to be taken only half seriously Apart from this, his best known expression of opinion, Bateson is the

author of a large amount of fine work in genetics and will rank high in the history of the subject

T H Morgan our leading American geneticist, is best known for his researches into the mechanism of Mendelian inheritance Through the statistical study of ratios and linkages of characters in the fruit fly *Drosophila* it has been possible to chart the localities of the deter miners or genes of at least 400 mutant characters He has shown that four linked groups of genes exist, corresponding to the four kinds of chromosomes of the germ cells, one of these groups is sex linked and is therefore to be assigned to the X-chromosome of the mutant male Two other large groups are to be located in the two large autosomes, and one very small group is assumed to be located in the microsome Not only have characters, or their determiners, been assigned to given chromosomes, but they have been located in a linear series on a given chromosome So accurately have these loci been determined that they may be used to predict unknown breeding ratios It would seem that when a theory serves so well that it may be used to predict the results of experiments such a theory must be founded on facts Morgan and his collaborators in genetics are now convinced that they have discovered the actual mechanism of heredity in the behavior of the chromosomes in maturation and fertilization and that it is unex pectedly simple Their views have aroused considerable opposition but they have apparently met successfully all attacks up to the present If it be true that the actual machinery of variation and heredity has been discovered we are farther along in our understanding of the causo-mechanical basis of evolution than we could have hoped to be at so early a date

HEREDITY AND SEX

Since Darwin s theory of sexual selection, sex has been a compli cating factor in evolutionary theories, and one of the chief advances of the present century has been in connection with the factors con trolling sex determination and sex differentiation. The evolution of sex has also been a subject for considerable research

It now appears that sex is an inherited Mendelian character, the determiner of which is carried in a definite chromosome or group of chromosomes Cytological examination of germ cells, under the able leadership of *E B Wilson*, has now made it certain that sex, if not directly the result of the presence or absence of specific chromosomes, at least is absolutely correlated with such chromosomes It appears, however, that the sex which is settled by the chromosome

mechanism at the time of fertilization may or may not realize its normal somatic differentiation, depending upon the presence or absence of the proper environment Cases are on record in which an individual germinally determined as a female may be caused to develop the secondary sexual characters of the male or even to pro duce sperms instead of eggs A great deal of extremely interesting work on sex control and sex reversals has been done within the last half-dozen years and new discoveries are being made almost daily In fact, it might be said that the genetic study of sex marks the high tide level of modern genetic advance

THE EXPERIMENTAL INDUCTION OF HEREDITARY VARIATIONS

With the problem of the mechanism of the heredity of individual differences solved at least in its more important essentials attention has gradually shifted to the problem as to how individual differences arise They seem to arise suddenly and as though of their own accord and the study of their heredity does not throw much light on the prob lem of their origin At the present time a massed attack is being made upon the problem of the mode or modes of origin of new hereditary characters The most striking success in the artificial induction of mutations has been obtained by *H F Muller* using as his material the already intensively studied fruit fly *Drosophila melanogaster* By the use of rather heavy doses of X rays he succeeded in increasing the fre quency of mutations about 1 500 per cent Nearly all of the mutations produced by this method were the same as those that occur spontane ously but many more occur in a given time

Many other investigators following Muller s methods have suc ceeded in greatly hastening the pace of mutation in various animals and plants The ability to produce such large numbers of mutants at will furnishes abundant material for genetic investigation and promises greatly to increase our knowledge of the intimate details of the mechan isms of variation and heredity

The most pressing problem of the present is that of discovering how and when genes act during the course of development in producing the characters of the organism Some progress has been made in this direction

THE RECENT ATTACK UPON EVOLUTION IN THE UNITED STATES

The recent highly advertised attack upon the validity of the principle of evolution by certain individuals and religious bodies is hardly to be considered as forming a part of the history of the science,

but it is significant as an influence that may serve either greatly to accelerate or to retard the progress of our science The writer's own experience is that the controversy has greatly enhanced popular interest in this subject, as evidenced by the growing demand for books on evolution and allied subjects and the marked increase in the numbers of students in the colleges who wish to elect courses along these lines

CONCLUDING REMARKS

Now that we have traced the evolution of the science of organic evolution from its crude beginnings among the Greeks up to the present we are in a position to go back and make a systematic study of some of the more important phases of evolutionary science Charles Darwin found it necessary to prove the fact of organic evolution before attempting to discover its causes His method of proof was to marshal a great array of facts which agree with the idea of descent with modification, and we shall follow Darwin's method in the subsequent chapters dealing with the evidences of evolution

NOTE —In the first half of the present historical account many short passages are presented in quotation marks without mentioning the source of the quotation In all such cases it will be understood that these passages are from H. F Osborn's book *From the Greeks to Darwin* (The Macmillan Company)

PART II

EVIDENCES OF ORGANIC EVOLUTION

CHAPTER III

IS ORGANIC EVOLUTION AN ESTABLISHED PRINCIPLE?

1 Is there definite proof of organic evolution?

2 If so, what is the nature of the proof?

3 What are the evidences of evolution, and in what ways do these bear witness that evolution has occurred and is still occurring?

Before presenting in any detail the several bodies of data that constitute the "evidences of evolution," let us anticipate a little by attempting to answer the three questions just propounded

1. Reluctant as he may be to admit it, honesty compels the evolutionist to admit that there is no absolute proof of organic evolution But, for that matter, there is no absolute proof of anything that depends on records of past events We have no absolute proof that Caesar or Napoleon once lived, or fought, or conquered All we have are the accounts left by the historians which we accept without question because they are the products of human thought and imagination There is no absolute proof for either of the more or less directly opposed theories of the origin of the material universe the 'nebular hypothesis of Laplace and the 'planetesimal hypothesis" of Chamberlin and Moulton Both of these theories rest upon exactly the same types of evidences as does the theory of organic evolution, viz, the amassing of facts which appear to be explicable on the assumption that the one or the other theory is true If all of the facts are in accord with it, and none are found that are incapable of being reconciled with it, a working hypothesis is said to have been advanced to the rank of a proved theory As yet it is impossible to say that either of these theories as to the origin of the universe has been proved Yet there is much less popular opposition to the acceptance of these theories as facts than there is to the general theory of organic evolution Similarly, there are certain widely accepted theories of the origin of the present conditions of the earth's crust, and its liquid and gaseous envelopes The accepted theory, as given us by Hutton and especially by Lyell is essentially an evolutionary theory and depends for its proof on almost exactly the same types of evidence as does that

of organic evolution The basis of the accepted theory of geological evolution is the uniformitarian doctrine ' of Lyell, which assumes that the key to the past lies in the present, that the changes that are going on today are of the same order and kind as those of the past, and, finally that there is neither beginning nor end to the earth's evolutionary history but that a slow and orderly development has gone on and will continue indefinitely The proof of this conception consists of an array of facts derived from a study of the earth's crust, including its stratified structure of traces of animal and plant life preserved in the rocks of observed changes in continental contours going on today of erosion going on in coasts and streams, and of a considerable array of facts derived from a study of other worlds than ours in the making The theory of geologic evolution meets with scarcely any opposition today although its foundations are no more securely based than are those of organic evolution

In a sense the proofs of the atomic, ionic, and electron theories are even less absolutely established than is that of organic evolution, because no one has ever seen nor ever can see an atom, an ion, or an electron Chemical and physical facts are rationalized by assuming the existence of these units with their various properties The only evidences of the existence of atoms, ions, and electrons appear in the facts that on the assumption that they exist, the whole array of observed chemical and physical phenomena are rationalized and bound together into a coherent, consistent, and intelligible system In other words with the atomic, ionic, and electron theories chemistry and physics are highly rational sciences without these theories the phenomena of physics and chemistry would be a hopeless hodgepodge Yet who would say that these fundamental theories are absolutely proved?

The only type of proof of phenomena that cannot be directly observed or that pertain to the remote past is *circumstantial* proof By analogy we conclude that certain changes took place thus and so in the past because we observe similar changes going on today Every past event has left a trace, and it is the task of the historian, antiquarian, or evolutionist to discover and to interpret these traces Sometimes the traces exist as vestiges in modern life and are meaningless unless related to their origin in the past The task of the student of organic evolution is to gather all of the traces of past changes both in living creatures today and in the preserved remains of creatures of the remote past A collection of traces of evolution involves many

apparently unrelated bodies of phenomena. There are evidences of evolution in the grouping of animals into phyla, classes, orders families, genera species, varieties, and races, in the homologies that exist in general structure and in particular organs between different *groups of animals and plants, in the orderly process of ontogeny* or embryonic development of the individual in actual blood relation ship, based upon chemical reactions, on the succession of extinct animals and plants found as fossils imbedded in the geologic strata in the present geographical distribution of the various groups of animals and plants, in the light of data derived from a study of geological changes, and finally, in experimental evolution which involves the observation under experimental control of changes in organisms and the origin of new varieties or elementary species

2 The nature of the proof of organic evolution, then, is this that, using the concept of organic evolution as a working hypothesis it has been possible to rationalize and render intelligible a vast array of observed phenomena the real facts upon which evolution rests *Thus classification (taxonomy), comparative anatomy embryology,* palaeontology, zoogeography and phytogeography, serology genetics become consistent and orderly sciences when based upon evolu tionary foundations, and when viewed in any other way they are thrown into the utmost confusion There is no other generalization known to man which is of the least value in giving these bodies of fact any sort of scientific coherence and unity In other words, the working hypothesis works and is therefore acceptable as truth until overthrown by a more workable hypothesis Not only does the hypothesis work, but with the steady accumulation of further facts the weight of evidence is now so great that it overcomes all intelligent opposition by its sheer mass There are no rival hypotheses except the outworn and completely refuted idea of special creation, now retained only by the ignorant the dogmatic, and the prejudiced

3 In answer to the question, "What are the evidences of evolution and in what ways do these bear witness that evolution has occurred and is still occurring?" we may present an ordered list of subjects that are to be taken up serially in detail In connection with each of these bodies of evidence the character of their witness-bearing will be discussed

Some of the evidences are more direct and freer from purely interpretative construction than others Some evidences are primary and foundational, some are in themselves rather inconclusive, but serve

to confirm other facts, and, when reinforced by other evidences, are themselves strongly substantiated Perhaps the crowning evidence of the truth of evolution is that all of these diverse bodies or phenomena invariably support one another and all point in the same direction and to the same conclusion, viz , that organic evolution is a fact

In the former edition of this book the evidences of evolution were presented in a somewhat arbitrary order, the evidences that seemed to furnish the most direct proof being, for pedagogical reasons presented first and the more controversial evidences last Experience, however, has shown that for an appreciation of the data from paleontology and from geographic distribution the student must have a knowledge of the principles of morphology (comparative anatomy) and of classification We have, therefore, changed the order of presentation of the evidences to one that has the authority of precedent The order of treatment will be as follows

I *The fundamental assumption underlying all the evidences*

II *Comparative anatomy* (*homologies and vestigial structures*) the evidence of the fact that structures in unlike organisms have a common plan and mode of origin that changes have occurred that are in some way related to changes in habit or environment

III *Classification* the evidence that the present groups of animals and plants have arisen by descent with modification '

IV *Serology* (*blood-precipitation tests*) the evidence that the chemical specificity of the blood parallels taxonomic specificity

V *Embryology* (*the doctrine of recapitulation*) the evidences that the embryonic development of the individual follows the main out lines of the evolutionary history of its ancestors

VI *Paleontology* the evidences afforded by a study of the distribution in time (vertical distribution in the earth's strata) of the fossil remains of extinct animals and plants

VII *Geographic distribution* the evidences afforded by present (also, to some extent past) horizontal distribution of contemporaneous animals and plants

VIII *Genetics* (*experimental evolution*) evidences that heritable variations have occurred under observation in large numbers and in many species of animals and plants and that new varieties of animals and plants have been produced by processes known to man and to a large extent controlled by him

CHAPTER IV

THE FUNDAMENTAL POSTULATE UNDERLYING ALL EVIDENCES OF EVOLUTION

Every science rests in last analysis upon certain postulates or justifiable assumptions certain verified or verifiable truths that must be admitted before any progress can be made in gaining a further understanding of the content of that science Geology for example must assume as valid the dynamical laws of Newton and the law of gravitation as well as basic laws of chemistry Biology assumes the validity of the laws of physics and chemistry for biology is the fundamental science of the transformations of matter and of energy in living matter but in addition there are also some biological postulates that seem to be so well established that they have come to be thought of as truisms

One of the truisms of biology is the familiar fact that like produces like How surprised one would be if sparrows had anything but sparrows for offspring or if two Caucasic parents were to have a Negro child! Now a careful survey of the situation reveals the fact that the only postulate the evolutionist needs is no more nor less than a logical extension of what the layman considers a truism or a self evident fact namely that fundamental structural resemblance signifies genetic relationship that generally speaking *the degree of closeness of structural resemblance runs essentially parallel with closeness of kinship* Most biologists would say that this is not merely a postulate but one of the best established laws of life However obvious the validity of this postulate may be it is the plain duty of one who attempts to justify the evolutionary principle to avoid taking any steps that are open to the least bit of valid criticism If we cannot rely upon this postulate which may be called the principle of homology we can make no sure progress in any attempt to establish the validity of the principle of evolution

The postulate we are now discussing is tantamount to an affirmation of the fact of *heredity* We rely upon this fact in our everyday life When we plant a certain kind of seed we expect to get a certain kind of plant when we breed a certain kind of dog we expect offspring

of the same breed It would be a freak of nature were we to discover any marked exception to the laws of heredity Furthermore, our ordinary daily contacts with other members of our own species have taught us that as a rule the more closely alike people are, the more closely are they related We recognize that children of the same family are more alike in their personal characteristics than are members of the same race not closely related Whenever we see two people whose resemblance is very great we assume a relatively close kinship Thus everyone has had the experience of meeting two people so strikingly alike that it is almost impossible to distinguish them apart, and of immediately assuming that such persons are identical, or duplicate twins Now the interesting thing about such twins is that they are vastly more closely related than are ordinary brothers and sisters, or even than are fraternal twins who are only brothers and sisters that happen to have been conceived and born simultaneously as the result of the fertilization of two egg cells For duplicate twins are the products of the early division into two equivalent parts of a single embryo derived from one fertilized egg No closer kinship can well be imagined than this for the two individuals bear the same relationship to each other as do the bilateral halves of one individual.

The writer has had an exceptional opportunity of determining the exact degree of resemblance existing between separate offspring derived from a single egg It so happens that a peculiar species of mammal, the nine banded armadillo of Texas, always gives birth to four young at a time These quadruplets are invariably all of the same sex in a litter and are nearly identical even in their finest anatomical details such as the numbers and arrangements of the plates and scales in the armor and the numbers of hairs in a given area of the skin. A detailed study of the embryonic history of this species has proved beyond any question that in every case the four young in a litter result from a very early division of a single embryo derived from a single fertilized egg (see Fig 32) Large numbers of sets of quadruplets were studied statistically to determine the exact degree of their resemblance to one another A comparison of over two hundred sets revealed the somewhat startling fact that on the average they were over 93 per cent identical (more technically, they showed a coefficient of correlation of over 93) The remarkable closeness of this degree of resemblance may be fully appreciated when it is realized that the only structural resemblance belonging to this order of closeness is that existing between the right and left antimeric halves of a single indi

vidual, such as the right and left sides of your own face or your two hands, and that the next degree of closeness of resemblance is that between siblings (brothers and sisters), who are only 50 per cent identical (having a coefficient of correlation of only .5), while cousins of various grades have proportionately lower and lower degrees of resemblance in exact ratio with their grades of kinship.

This, then, is a crucial test of the validity of the postulate that closeness of resemblance is in proportion to closeness of kinship, for we have in identical twins and in armadillo quadruplets the closest resemblance associated with the closest possible genetic relationship, and we also see that there is an exact proportion between all other known grades of kinship and their relative degree of resemblance.

Employing the principle of homology in a somewhat broader way, and in a way that is hardly likely to be questioned even by the most captious, we account for the common possession of certain structural peculiarities by all members of a given kind or species of animal or plant by saying that such characters have been derived from a common ancestor. It is only a short step in logic to conclude that two similar kinds or species of animal have been derived one from the other or both from a common ancestral species. Once having taken this step, we are on the road that leads inevitably to an evolutionary interpretation of natural groups. If the principle of heredity holds for siblings (offspring of the same parents), for races, for species, where are we to draw the line? It does not seem reasonable to admit that structural resemblances between siblings, between races, between species, are accounted for as the product of heredity, and to deny that equally plain resemblances of essentially the same sort among the species of a genus or among the genera of a family have a similar hereditary basis. It is logically impossible to draw the line at any level of organic classification and say that structural resemblance is the product of heredity up to such and such a level, but that beyond this arbitrarily chosen point heredity ceases to operate.

The principle of heredity and its necessary implications constitute the only postulate that is necessary for the evolutionist to make in order to go ahead on a sound basis with a presentation of the evidences of evolution. Give him this one point, and he asks no further concessions. *And this is not so much of a concession as it might* seem at first blush, for the special creationist assumes more potency for heredity than does the evolutionist, since he believes in descent without modification, a sort of stereotyped heredity, slavishly duplicating

forever a fixed set of structural patterns without variation or improvement Since then both special creationist and evolutionist find it equally necessary to assume the principle of heredity, there should be little argument on this score But let the reader beware at this point in the discussion for if he admits the postulates already presented—and how can he help but admit them?—he cannot avoid the inevitable conclusion that the theory of descent with modification is the only reasonable explanation of organic resemblances and differences.

HOMOLOGY VERSUS ANALOGY

Much difficulty in connection with the study of resemblances and differences in animal and plants is occasioned by a failure to understand the fact that there are two kinds of resemblances and differences Structures that are similar in anatomical detail and in their mode of embryonic origin irrespective of whether they perform the same or different functions are known as *homologous* The test of homological equivalence is a study of the anatomical details of the adult structure followed by a study of the developmental history of the part in question If the part under examination be a bone, for example, this bone must have a certain relation to the other bones, must occur in a certain part of the body, must be supplied with certain muscle attachments, in order to be considered homologous with another bone that has the same relations If two structures have the same anatomical relations and arise from equivalent embryonic rudiments they are said to be homologous in spite of small or great differences in relative size, appearance or function If structures are homologous it is believed that they represent the same hereditary units and that these equivalent hereditary units have been derived from the same or similar ancestors

Analogous structures are of an entirely different sort They may be more or less superficially alike in form or in function, usually in both, though anatomically quite different As an example of analogous structures let us examine the three types of aquatic vertebrates shown in Figure 80 These three kinds of vertebrates, one a fish, one a reptile, and the third a mammal might be mistaken by the casual observer to be all fishes of different kinds All have the same fusiform body with lines best adapted for swift locomotion in the water, all have median paired and caudal fins all swim in about the same way Yet the resemblance is only skin-deep, as it were, for beneath the surface the one is all fish, the second all reptile, and the third all mammal The structures that look alike and function alike are, from the stand-

point of anatomical relations and embryonic derivation, entirely different. The resemblances which are so obvious superficially are examples of *analogy*, not of homology, and are the result of molding unlike materials into a semblance of likeness in adaptation to a common environment. Analogous structures, while not considered as evidences of kinship, are strong evidences of descent with modification, for their very existence implies that they have been changed from a former condition to one in which they are adapted to a new medium. To illustrate this point, call to mind that both the ichythyosaur and the porpoise (Fig. 80, *B* and *C*) belong to groups that are fundamentally terrestrial air breathing vertebrates, and that whatever they have that is fishlike must be interpreted as adaptive modifications for aquatic life. This type of conception and the way in which it bears witness for organic evolution is well brought out in the next chapter by George John Romanes, a chapter that for a generation has been considered a classic. A few of the statements in this chapter would, in all probability, be somewhat altered if the author were to rewrite it in the light of newer knowledge, but on the whole the statements made would still have the support of the most critical of modern anatomists.

CHAPTER V

EVIDENCES FROM MORPHOLOGY (COMPARATIVE ANATOMY)

GEORGE J ROMANES[1]

The theory of evolution supposes that hereditary characters admit of being slowly modified wherever their modification will render an organism better suited to a change in its conditions of life. Let us then observe the evidence which we have of such adaptive modifications of structure in cases where the need of such modification is apparent. We may begin by again taking the case of the whales and porpoises. The theory of evolution infers from the whole structure of these animals that their progenitors must have been terrestrial quadrupeds of some kind which gradually became more and more aquatic in their habits. Now the change in the conditions of their life thus brought about would have rendered desirable great modifications of structure. These changes would have begun by affecting the least typical—that is the least strongly inherited—structures such as the skin claws and teeth. But as time went on the adaptations would have extended to more typical structures until the shape of the body would have become affected by the bones and muscles required for terrestrial locomotion becoming better adapted for aquatic locomotion and the whole outline of the animal more fish like in shape. This is the stage which we actually observe in the seals where the hind legs although retaining all their typical bones have become shortened up almost to rudiments and directed backwards so as to be of no use for walking while serving to complete the fish like taper of the body (Fig 1). But in the whales the modification has gone further than this so that the hind legs have ceased to be apparent externally and are only represented internally—and even this only in some species—by remnants so rudimentary that it is difficult to make out with certainty the homologies of the bones moreover the head and the whole body have become completely fish like in shape (Fig 12). But profound as are these alterations they affect only

[1] From G J Romanes *Darwin and after Darwin* (copyright 1892). Used by special permission of the publishers The Open Court Publishing Company

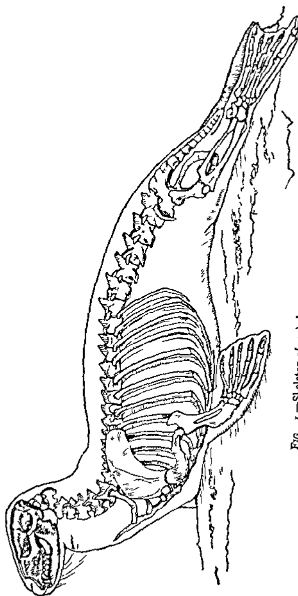


FIG 1 —Skeleton of seal, [illegible] nat size (From Romanes)

those parts of the organism which it was for the benefit of the organism to have altered, so that it might be adapted to an aquatic mode of existence Thus the arm which is used as a fin still retains the bones of the shoulder, fore-arm wrist and fingers although they are all enclosed in a fin shaped sack so as to render them useless for any purpose other than swimming (Fig 3) Similarly, the head, although it so closely resembles the head of a fish in shape, still retains the bones of the mammalian skull in their proper anatomical relations to one another but modified in form so as to offer the least possible resistance to the water In short it may be said that all the modifications have been effected with the least possible divergence from the typical mammalian type, which is compatible with securing so perfect an adaptation to a purely aquatic mode of life

Now I have chosen the case of the whale and porpoise group, because they offer so extreme an example of profound modification of structure in adaptation to changed conditions of life But the same thing may be seen in hundreds and hundreds of other cases For instance to confine our attention to the arm, not only is the limb modified in the whale for swimming but in another mammal—the bat—it is modified for flying, by having the fingers enormously elongated and overspread with a membranous web

In birds again the arm is modified for flight in a wholly different way—the fingers here being very short and all run together, while the chief expanse of the wing is composed of the shoulder and forearm In frogs and lizards, again, we find hands more like our own, but in an extinct species of flying reptile the modification was extreme, the wing having been formed by a prodigious elongation of the fifth finger and a membrane spread over it and the rest of the hand (Fig 4) Lastly, in serpents the hand and arm have disappeared altogether

Thus, even if we confine our attention to a single organ, how wonderful are the modifications which it is seen to undergo, although never losing its typical character Everywhere we find the distinction between homology and analogy which was explained in the last chapter—the distinction that is, between correspondence of structure and correspondence of function On the one hand, we meet with structures which are perfectly homologous and yet in no way analogous, the structural elements remain, but are profoundly modified so as to perform wholly different functions On the other hand, we meet with structures which are perfectly analogous, and yet in no way homologous, totally different structures are modified

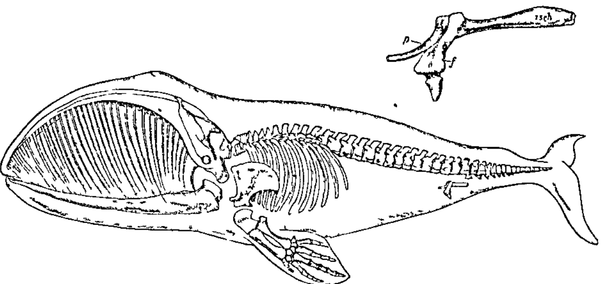


FIG 2.—Skeleton of Greenland whale 1/100 nat size The rudimentary bones of the pelvis are shown on a large scale in the upper drawing (*From Romanes after Flower*)

to perform the same functions How then are we to explain these things? By design manifested in special creation or by descent with adaptive modification? If it is said by design manifested in special creation we must suppose that the Deity formed an archetypal plan of certain structures and that he determined to adhere to this plan through all the modifications which those structures exhibit But, if so why is it that some structures are selected as typical and not others? Why should the vertebral skeleton for instance, be tortured

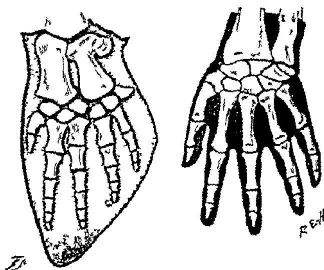


Fig 3 —Paddle of whale compared with hand of man (*From Romanes*)

into every conceivable variety of modification in order to subserve as great a variety of functions while another structure, such as the eye is made in different sub kingdoms on fundamentally different plans notwithstanding that it has throughout to perform the same function? Will any one have the hardihood to assert that in the case of the skeleton the Deity has endeavored to show his ingenuity, by the manifold functions to which he has made the same structure subservient while in the case of the eye he has endeavored to show his resources by the manifold structures which he has adapted to serve the same function? If so, it becomes a most unfortunate circumstance that, throughout both the vegetable and animal kingdoms all cases which can be pointed to as showing ingenious adaptation of the

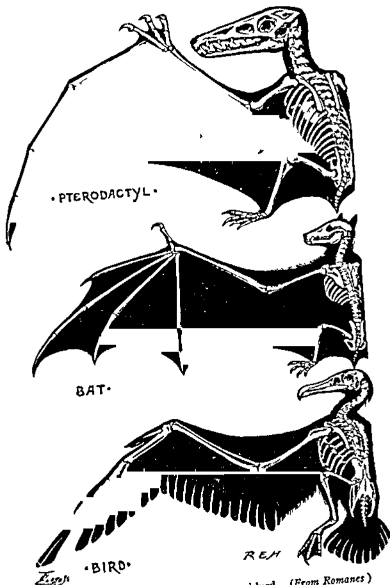


FIG 4—Wing of reptile, mammal and bird (*From Romanes*)

same typical structure to the performance of widely different functions—or cases of homology without analogy—are cases which come within the limits of the same natural group of plants and animals, and therefore admit of being equally well explained by descent from a common ancestry while all cases of widely different structures performing the same function—or cases of analogy without homology, are to be found in different groups of plants or animals, and are therefore suggestive of independent variations arising in the different lines of hereditary descent

To take a specific illustration The octopus, or devil fish, belongs to a widely different class of animals from a true fish, and yet its eye, in general appearance looks wonderfully like the eye of a true fish Now Mr Mivart pointed to this fact as a great difficulty in the way of the theory of evolution by natural selection, because it must clearly be a most improbable thing that so complicated a structure as the eye of a fish should happen to be arrived at through each of two totally different lines of descent And this difficulty would, indeed, be a formidable one to the theory of evolution, if the similarity were not only analogical but homological Unfortunately for the objection however Darwin clearly showed in his reply that in no one anatomical or homologous feature do the two structures resemble one another, so that, in point of fact the two organs do not resemble one another in any particular further than it is necessary that they should, if both are to be analogous or to serve the same function as organs of sight But now, suppose that this had not been the case and that the two structures besides presenting the necessary superficial or analogical resemblance, had also presented an anatomical or homologous resemblance, with what force might it have then been urged,—your hypothesis of hereditary descent with progressive modification being here excluded by the fact that the animals compared belong to two widely different branches of the tree of life how are we to explain the identity of type manifested by these two complicated organs of vision? The only hypothesis open to us is intelligent adherence to an ideal plan or mechanism But as this cannot now be urged in any comparable case throughout the whole organic world we may, on the other hand present it as a most significant fact that while within the limits of the same large branch of the tree of life we constantly find the same typical structures modified so as to perform very different functions we never find any of these particular types of structure in other large branches of the tree That is to say, we never find typical structures

appearing except in cases where their presence may be explained by the hypothesis of hereditary descent, while in thousands of such cases we find these structures undergoing every conceivable variety of adaptive modification

Consequently, special creationists must fall back upon another position and say,—Well, but it may have pleased the Deity to form a certain number of ideal types, and never to have allowed the structures occurring in one type to appear in any of the others We answer,—Undoubtedly such may have been the case but, if so, it is a most unfortunate thing for your theory, because the fact implies that the Deity has planned his types in such a way as to suggest the counter theory of descent For instance, it would seem most capricious on the part of the Deity to have made the eyes of an innumerable number of fish on exactly the same ideal type, and then to have made the eye of the octopus so exactly like these other eyes in superficial appearance as to deceive so accomplished a naturalist as Mr Mivart and yet to have taken scrupulous care that in no one ideal particular should the one type resemble the other However adopting for the sake of argument this great assumption, let us suppose that God did lay *down these arbitrary rules for his own guidance in creation and* then let us see to what the assumption leads If the Deity formed a certain number of ideal types, and determined that on no account should he allow any part of one type to appear in any part of another surely we should expect that within the limits of the same type the same typical structures should always be present. Thus, remember what efforts, so to speak, have been made to maintain the uniformity of type in the case of the fore limb as previously explained, and should we not expect that in other and similar cases a similar method should have been followed? Yet we repeatedly find that this is not the case Even in the whale as we have seen, the hind limbs are either altogether absent or dwindled almost to nothing, and it is impossible to see in what respects the hind limbs are of any less ideal value than the fore limbs—which are carefully preserved in all vertebrated animals except the snake, and the extinct Dinornis where again we meet in this particular with a sudden and sublime indifference to the maintenance of a typical structure (Fig 5) Now I say that if the theory *of ideal types is true, we have in these facts evidence of a most unreasonable* inconsistency But the theory of descent with continued adaptive modification fully explains all the known cases, for in every case the degree of divergence from the typical structure which an

organism presents corresponds in a general way with the length of time during which the divergence has been going on Thus we

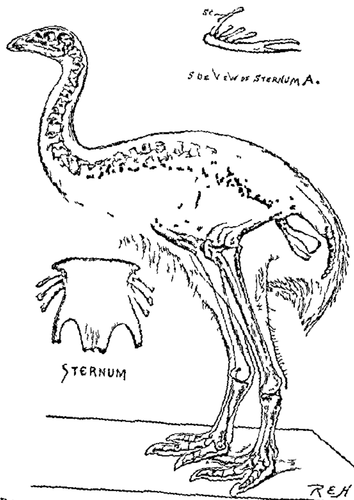


FIG 5 —Skeleton of *Dinornis gravis* $\frac{1}{18}$ nat size Drawn from nature (British Museum) As separate cuts on a larger scale are shown, (1) the sternum as this appears in mounted specimens and (2) the same in profile with its (hypothetical) scapulo coracoid attached (*From Romanes*)

scarcely ever meet with any great departure from the typical form with respect to one of the organs without some of the other organs being so far modified as of themselves to indicate, on the supposition

of descent with modification that the animal or plant must have been subject to the modifying influences for an enormously long series of generations And this combined testimony of a number of organs in the same organism is what the theory of descent would lead us to expect, while the rival theory of design can offer no explanation of the fact, that when one organ shows a conspicuous departure from the supposed ideal type, some of the other organs in the same organism should tend to keep it company by doing likewise

As an illustration both of this and of other points which have been mentioned, I may draw attention to what seems to me a particularly suggestive case So-called soldier- or hermit-crabs are crabs which have adopted the habit of appropriating the empty shells of mollusks In association with this peculiar habit, the structure of these animals differs very greatly from that of all other crabs In particular, the hinder part of the body, which occupies the mollusk shell, and which therefore has ceased to require any hard covering of its own, has been suffered to lose its calcareous integument, and presents a soft fleshy character, quite unlike that of the most exposed parts of the animal Moreover, this soft fleshy part of the creature is especially adapted to the particular requirements of the creature by having its lateral appendages—i e, appendages which in other crustacea perform the function of legs— modified so as to act as claspers to the inside of the mollusk shell, while the tail end of the part in question is twisted into the form of a spiral which fits into the spiral of the mollusk shell Now, in Keeling Island there is a large kind of crab called *Birgus latro*, which lives upon land and there feeds upon cocoa nuts The whole structure of this crab, it seems to me, unmistakably resembles the structure of a hermit-crab (Fig 6) Yet this crab neither lives in the shell of a mollusk nor is the hinder part of its body in the soft and fleshy condition just described, on the contrary, it is covered with a hard integument like all the other parts of the animal Consequently, I think we may infer that the ancestors of *Birgus* were hermit crabs living in mollusk shells, but that their descendants gradually relinquished this habit as they gradually became more and more terrestrial, while, concurrently with these changes in habit, the originally soft posterior parts acquired a hard protective covering to take the place of that which was formerly supplied by a mollusk shell. So that, if so we now have, within the limits of a single organism evidence of a whole series of morphological changes in the past history of its species First, there must have been the great change from an

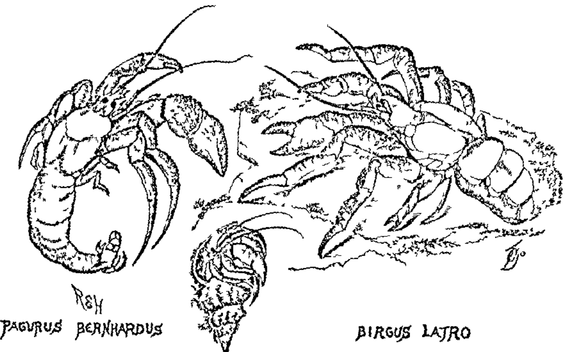


FIG 6—Hermit crabs compared with cocoa nut crab On the left of the illustration one hermit crab is represented as occupying a mollusk shell, and another (larger specimen) as it appears when withdrawn from such a shell On the right of the illustration the cocoa nut crab is represented in its natural habitat on land When full grown, however, it is much larger than our hermit crabs The latter are drawn from life, the former from a

ordinary crab to a hermit-crab in all the respects previously pointed out. Next, there must have been the change back again from a hermit-crab to an ordinary crab, so far as living without the necessity of a mollusk shell is concerned. From an evolutionary point of view therefore, we appear to have in the existing structure of *Birgus* a morphological record of all these changes, and one which gives us a reasonable explanation of why the animal presents the extraordinary appearance which it does But, on the theory of special creation it is inexplicable why this land-crab should have been formed on the pattern of a hermit-crab, when it never has need to enter the shell of a mollusk In other words, its peculiar structure is not especially in keeping with its present habits, although so curiously allied to the similar structure of certain other crabs of totally different habits, in relation to which the peculiarities are of plain and obvious significance

I will devote the remainder of this chapter to considering another branch of the argument from morphology, to which the case of *Birgus* serves as a suitable introduction I mean the argument from rudimentary structures

Throughout both the animal and vegetable kingdoms we constantly meet with dwarfed and useless representatives of organs which in other and allied kinds of animals and plants are of large size and functional utility Thus, for instance the unborn whale has rudimentary teeth, which are never destined to cut the gums, and throughout its life this animal retains, in a similarly rudimentary condition, a number of organs which never could have been of use to any kind of creature save a terrestrial quadruped The whole anatomy of its internal ear, for example, has reference to hearing in air, as Hunter long ago remarked, "is constructed upon the same principle as in the quadruped , yet, as Owen says, the outer opening and passage leading therefrom to the tympanum can rarely be affected by sonorous vibrations of the atmosphere and indeed they are reduced, or have degenerated, to a degree which makes it difficult to conceive how such vibrations can be propagated to the ear drum during the brief moments in which the opening may be raised above the water '

Now, rudimentary organs of this kind are of such frequent occurrence, that almost every species presents one or more of them—usually, indeed, a considerable number How, then, are they to be accounted for? Of course the theory of descent with adaptive modification has a simple answer to supply—namely, that when from

changed conditions of life an organ which was previously useful becomes useless it will be suffered to dwindle away in successive generations under the influence of certain natural causes which we shall have to consider in future chapters On the other hand the theory of special creation can only maintain that these rudiments are formed for the sake of adhering to an ideal type Now, here again the former theory appears to be triumphant over the latter, for without waiting to dispute the wisdom of making dwarfed and useless structures merely for the whimsical motive assigned surely if such a

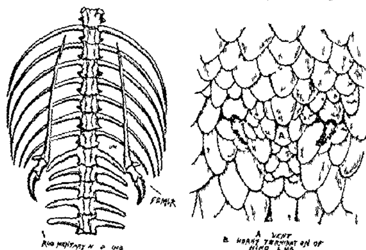


Fig 7 Rudimentary or vestigial hind limbs of python as exhibited in the skeleton and on the external surface of the animal Drawn from nature ½ nat size (*From Romanes*)

method were adopted in so many cases we should expect that in consistency it would be adopted in all cases This reasonable expectation however is far from being realized We have already seen that in numberless cases such as that of the fore limbs of serpents *no* vestige of a rudiment is present But the vacillating policy in the matter of rudiments does not end here for *it* is shown in a still more aggravated form where within the limits of the same natural groups of organisms a rudiment is sometimes present and sometimes absent. For instance although in nearly all the numerous species of snakes there are no vestiges of limbs in the Python we find very tiny rudiments of the hind limbs (Fig 7) Now, is it a worthy conception of Deity that while neglecting to maintain his unity of ideal in the case of

nearly all the numerous species of snakes, he should have added a tiny rudiment in the case of the Python—and even in that case should have maintained his ideal very inefficiently, inasmuch as only two limbs, instead of four, are represented? How much more reasonable is the naturalistic interpretation, for here the very irregularity of their appearance in different species, which constitutes rudimentary structures one of the crowning difficulties to the theory of special design, *furnishes the best possible evidence in favour of hereditary*

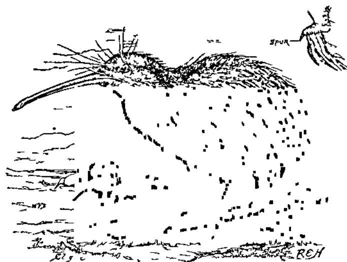


FIG 8—*Apteryx australis* Drawn from life in the Zoological Gardens ¼ nat size The external wing is drawn to a scale in the upper part of the cut The surroundings are supplied from the most recent descriptions (*From Romanes*)

descent, seeing that this irregularity then becomes what may be termed the anticipated expression of progressive dwindling due to inutility Thus, for example, to return to the case of wings, we have already seen that in an extinct genus of bird, *Dinornis*, these organs were reduced to such an extent as to leave it still doubtful whether so much as the tiny rudiment hypothetically supplied to Figure 5 was present in all the species And here is another well known case of another genus of still existing bird, which as was the case with *Dinornis*, occurs only in New Zealand (Fig 8) Upon this island there are no four footed enemies—either existing or extinct—to escape from which the wings of birds would be of any service Conse-

limestone caverns under nearly the same climate in the two continents of America and Europe so that in accordance with the theory of special creation very close similarity in the organizations of the two sets of faunas might have been expected But instead of this the affinities of these two sets of faunas are with those of their respective continents—as of course they ought to be on the theory of evolution Again what would have been the sense of creating the useless foot stalks for the imaginary support of absent eyes not to mention all the other various grades of degeneration in other cases? So that, upon the whole if we agree with the late Professor Agassiz in regarding these cave animals as furnishing a crucial test between the rival theories of creation and evolution we must further conclude that the whole body of evidence which they now furnish is weighing on the side of evolution

So much then for a few special instances of what Darwin called rudimentary structures but what may be more descriptively designated—in accordance with the theory of descent—obsolescent or vestigial structures It is however of great importance to add that these structures are of such general occurrence throughout both the vegetable and animal kingdoms that as Darwin has observed, it is almost impossible to point to a single species which does not present one or more of them. In other words it is almost impossible to find a single species which does not in this way bear some record of its own descent from other species and the more closely the structure of any species is examined anatomically the more numerous are such records found to be Thus for example of all organisms that of man has been most minutely investigated by anatomists and therefore I think it will be instructive to conclude this chapter by giving a list of the more noteworthy vestigial structures which are known to occur in the human body I will take only those which are found in adult man reserving for the next chapter those which occur in a transitory manner during earlier periods of his life But even as thus restricted, the number of obsolescent structures which we all present in our own person is so remarkable, that their combined testimony to our descent from a quadrumanous ancestry appears to me in itself conclusive I mean that even if these structures stood alone or apart from any more general evidences of our family relationships they would be sufficient to prove our parentage Nevertheless it is desirable to remark that of course these special evidences which I am about to detail do not stand alone. Not only is there the general analogy

furnished by the general proof of evolution elsewhere, but there is likewise the more special correspondence between the whole of our anatomy and that of our nearest zoological allies Now the force of this latter consideration is so enormous that no one who has not studied human anatomy can be in a position to appreciate it For without special study it is impossible to form any adequate idea of the intricacy of structure which is presented by the human form Yet it is found that this enormously intricate organisation is repeated in all its details in the bodies of the higher apes There is no bone, muscle, nerve, or vessel of any importance in the one which is not answered to by the other Hence there are hundreds of thousands of instances of the most detailed correspondence, without there being any instances to the contrary, if we pay due regard to vestigial characters The entire corporeal structure of man is an exact anatomical copy of that which we find in the ape

My object, then, here is to limit attention to those features of our corporeal structure which, having become useless on account of our change in attitude and habits, are in the process of becoming obsolete, and therefore occur as mere vestigial records of a former state of things For example, throughout the vertebrated series, from fish to mammals, there occurs in the inner corner of the eye a semi transparent eye-lid, which is called the nictitating membrane The object of this structure is to sweep rapidly, every now and then over the external surface of the eye apparently in order to keep the surface clean But although the membrane occurs in all classes of the sub kingdom, it is more prevalent in some than in others—e g , in birds than in mammals Even, however, where it does not occur of a size and mobility to be of any use, it is usually represented, in animals above fishes, by a functionless rudiment, as here depicted in the case of man (Fig 9)

Now the organisation of man presents so many vestigial structures thus referring to various stages of his long ancestral history, that it would be tedious so much as to enumerate them Therefore I will yet further limit the list of vestigial structures to be given as examples by not only restricting these to cases which occur in our own organisa tion, but of them I shall mention only such as refer us to the very last stage of our ancestral history—viz , structures which have become obsolescent since the time when our distinctively human branch of the family tree diverged from that of our immediate forefathers, the Quadrumana

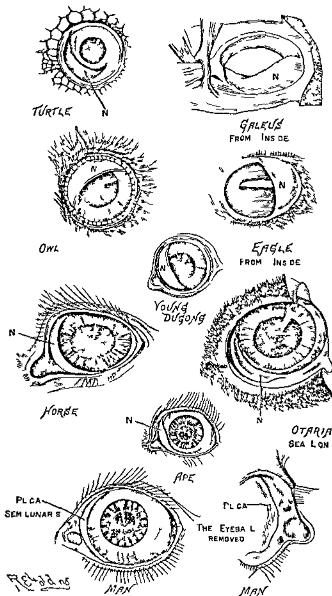


FIG. 9.—Illustrations of the nictitating membrane in the various animals named, drawn from nature. The letter *N* indicates the membrane in each case. In man it is called the *plica semilunaris* and is represented in the two lower drawings under this name. In the case of the shark (*Galeus*) the muscular membrane is shown as dissected. (*From Romanes.*)

1 Muscles of the external ear —These, which are of large size and functional use in quadrupeds, we retain in a dwindled and useless condition (Fig 10) This is likewise the case in anthropoid apes but in not a few other Quadrumana (e g baboons, macacus, magots, etc) degeneration has not proceeded so far, and the ears are voluntarily movable

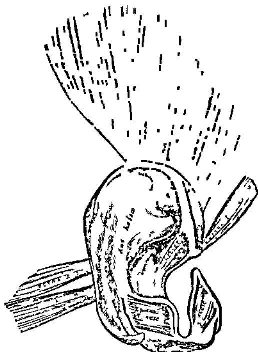


Fig 10 —Rudimentary or vestigial and useless muscles of the human ear (*From Roma cs after Gray*)

2 Panniculus carnosis —A large number of the mammalia are able to move their skin by means of subcutaneous muscle, as we see, for instance in a horse when thus protecting himself against the sucking of flies We in common with the Quadrumana, possess an active remnant of such a muscle in the skin of the forehead, whereby *we draw up the eyebrows but we are no longer able to use other* considerable remnants of it in the scalp and elsewhere —or more correctly it is rarely that we meet with persons who can But most of the Quadrumana (including the anthropoids) are still able to do so

There are also many other vestigial muscles, which occur only in a small percentage of human beings, but which, when they do occur, present unmistakable homologies with normal muscles in some of the Quadrumana and still lower animals

3 Feet —It is observable that in the infant the feet have a strong reflection inwards, so that the soles in considerable measure face one another This peculiarity, which is even more marked in the embryo than in the infant, and which becomes gradually less and



FIG 11 —Portrait of a young gorilla (*From Romanes after Hartmann*)

less conspicuous even before the child begins to walk, appears to me a highly suggestive peculiarity For it plainly refers to the condition of things in the Quadrumana, seeing that in all these animals the feet are similarly curved inwards, to facilitate the grasping of branches And even when walking on the ground apes and monkeys employ to a great extent the outside edges of their feet, as does also a child when learning to walk The feet of a young child are also extraordinarily mobile in all directions as are those of apes In order to show these points, I here introduce comparative drawings of a young ape and the

lower extremities of a still younger child These drawings, moreover, serve at the same time to illustrate two other vestigial characters, which have often been previously noticed with regard to the infant's foot I allude to the incurved form of the legs and the lateral extension of the great toe, whereby it approaches the thumb like character of this organ in the Quadrumana As in the case of the incurved position of the legs and feet so in this case of the lateral extensibility of the great toe, the peculiarity is even more marked in embryonic



FIG 12 —Lower extremities of a young child Drawn from life when the mob le feet were for a short time at rest in a position of extreme inflection (*From Romanes*)

than in infant life For, as Professor Wyman has remarked with regard to the foetus when about an inch in length, ' The great toe is shorter than the others and, instead of being parallel to them, is projected at an angle from the side of the foot, thus corresponding with the permanent condition of this part in the Quadrumana " So that this organ, which according to Owen ' is perhaps the most characteristic peculiarity of the human structure when traced back to the early stages of its development is found to present a notably less degree of peculiarity

4 Hands —Dr Louis Robinson has recently observed that the grasping power of the whole human hand is so surprisingly great at birth and during the first few weeks of infancy as to be far in excess of present requirements on the part of a young child Hence he concludes that it refers us to our quadrumanous ancestry—the young of anthropoid apes being endowed with similar powers of grasping in order to hold on to the hair of the mother when she is using her arms for the purposes of locomotion This inference appears to me justifiable

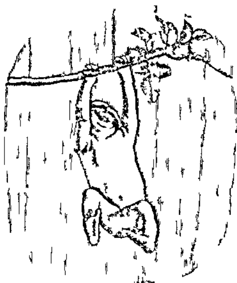


FIG 13 —A
minutes
duced from
Rob nson

inasmuch as no other explanation can be given of the comparatively inordinate muscular force of an infant s grip For experiments showed that very young babies are able to support their own weight by hold ng on to a horizontal bar for a period varying from one half to more than two minutes With l kind permission I here reproduce one of Dr Robinson s instantaneous and hitherto unpublished photographs of a very young infant This photograph was taken after the above paragraph (3) was written and I introduce it here because it serves to show incidentally—and perhaps even better than the preced ng figure—the points there mentioned with regard

to the feet and great toes Again, as Dr Robinson observes, the attitude, and the disproportionately large development of the arms as compared with the legs give all the photographs a striking resemblance to a picture of the chimpanzee "Sally" at the Zoological Gardens For "invariably the thighs are bent nearly at right angles to the body, and in no case did the lower limbs hang down and take the attitude of the erect position" He adds, "In many cases no sign of distress is evinced, and no cry uttered, until the grasp begins to give way"

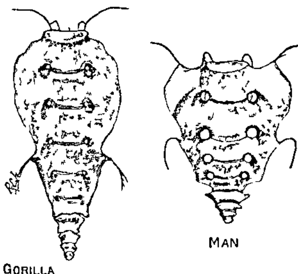


FIG 14 —Sacrum of gorilla compared with that of man showing rudimentary tail bones of each Drawn from nature (*From Romanes*)

5 Tail —The absence of a tail in man is popularly supposed to constitute a difficulty against the doctrine of his quadrumanous descent As a matter of fact, however, the absence of an external tail in man is precisely what this doctrine would expect seeing that the nearest allies of man in the quadrumanous series are likewise destitute of an external tail Far, then from this deficiency in man constituting any difficulty to be accounted for, if the case were not so—i e, if man did possess an external tail,—the difficulty would be to understand how he had managed to retain an organ which had been renounced by his most recent ancestors Nevertheless, as the anthro-

poid apes continue to present the rudimentary vestiges of a tail in a few caudal vertebrae below the integuments, we might well expect to find a similar state of matters in the case of man And this is just

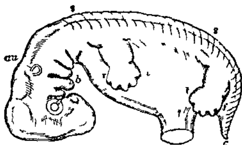


FIG 15 —Diagrammatic outline of the human embryo when about seven weeks old showing the relations of the limbs and tail to the trunk (*After Allen Thompson*) *r* the radial and *u* the ulnar border of the hand and forearm *t* the tibial and *f* the fibular border of the foot and lower leg *au* ear *u* spinal cord *u* umbilical cord *b* bronchial gill slits *c* tail (*From Romanes*)

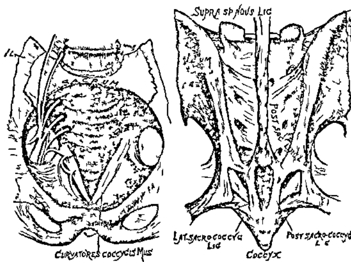


FIG 16 Front and back view of adult human sacrum showing abnormal persistence of vestigial tail muscles (*From Romanes*)

what we do find, as a glance at these two comparative illustrations will show (Fig 14) Moreover, during embryonic life, both of the anthropoid apes and of man, the tail much more closely resembles

that of the lower kinds of quadrumanous animals from which these higher representatives of the group have descended For at a certain stage of embryonic life the tail, both of apes and of human beings, is

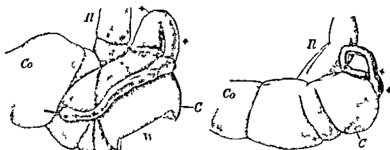


FIG 17 —Appendix vermiformis in orang and in man *Il* ilium *Co* colon *C* coecum W, a window cut in the wall of the coecum *xxx* the appendix (*From Romanes*)

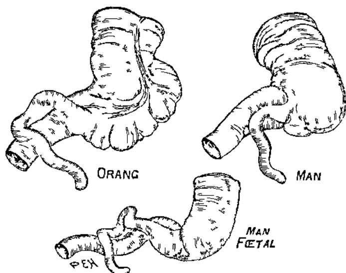


FIG 18 —The same showing variation in the orang (*From Romanes*)

actually longer than the legs (see Fig 15) And at this stage of development also the tail admits of being moved by muscles which later on dwindle away Occasionally however these muscles persist and are then described by anatomists as abnormalities The illustra

tions on page 82 (Fig 16) serve to show the muscles in question when thus found in adult man

6 Vermiform appendix of the coecum —This is of large size and functional use in the process of digestion among many herbivorous animals while in man it is not only too small to serve any such purpose but is even a source of danger to life—many persons dying every year from inflammation set up by the lodgement in this blind tube of fruit stones etc

In the orang it is longer than in man (Fig 17) as it is also in the human foetus proportionally compared with the adult (Fig 18) In some of the lower herbivorous animals it is longer than the entire body

Like the vestigial structures in general however this one is highly variable Thus Figure 18 serves to show that it may sometimes be almost as short in the orang as it normally is in man—both the human subjects of this illustration having been normal

7 Ear —Mr Darwin writes

The celebrated sculptor Mr Woolner informs me of one little peculiarity in the external ear which he has often observed both in men and women The peculiarity consists in a little blunt point projecting from the inwardly folded margin or helix When present it is developed at birth and according to Professor Ludwig Meyer more frequently in man than in woman Mr Woolner made an exact model of one such case and sent me the accompanying drawing [Fig 19] The helix obviously consists of the extreme margin of the ear folded inwards and the folding appears to be in some manner connected with the whole external ear being permanently pressed backwards In many monkeys which do not stand high in the order as baboons and some species of macacus the upper portion of the ear is slightly pointed and the margin is not at all folded inwards but if the margin were to be thus folded a slight point would necessarily project towards the centre In Figure 20 is shown an accurate copy of a photograph of the foetus of an orang (kindly sent me by Dr Nitsche) in which it may be seen how different the pointed outline of the ear is at this period from its adult condition, when it bears a close general



FIG 19 —Human ear modeled and drawn by Mr Woolner *a* the projecting point (*From Romanes*)

resemblance to that of man (including even the occasional appearance of the projecting point shown in the preceding woodcut) It is evident that the folding over of the tip of such an ear, unless it is changed greatly during its further development, would give rise to a point projecting inwards "[1]

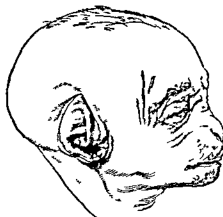


FIG 20 —Foetus of an orang Exact copy of a photograph showing the form of ear at this early stage (*From Romanes*)

The woodcut on page 86 (Fig 21) serves still further to show vestigial resemblances between the human ear and that of apes The last two figures illustrate the general resemblance between the normal ear of foetal man and the ear of an adult orangoutang The other two figures on the lower line are intended to exhibit occasional modifications of the adult human ear, which approximate simian characters somewhat more closely than does the normal type It will be observed that in their comparatively small lobes these ears resemble those of all the apes, and that while the outer margin of one is not unlike that of the Barbary ape, the outer margin of the other follows those of the chimpanzee and orang Of course it would be easy to select individual human ears which present either of these characters in a more pronounced degree, but these ears have been chosen as models because they present both characters in conjunction The upper row of figures likewise shows the close similarity of hair tracts, and the direction of growth on the part of the hair itself, in cases where the human hair happens to be of an abnormally hirsute character But this particular instance (which I do not think has been previously noticed) introduces us to the subject of hair and hair growth, in general

8 Hair —Adult man presents rudimentary hairs over most parts of the body Wallace has sought to draw a refined distinction between this vestigial coating and the useful coating of quadrumanous animals, in the absence of the former from the human back But even

[1] *Descent of Man* (2d ed), pp 15–16

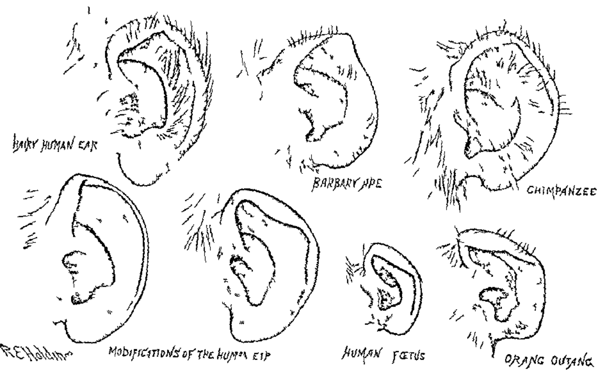


Fig 21 —Vestigial character of human ears Drawn from nature (*From Romanes*)

this refined distinction does not hold On the one hand, the comparatively hairless chimpanzee which died last year in the Zoological Gardens (*T calvus*) was remarkably denuded over the back, and, on the other hand, men who present a considerable development of hair over the rest of their bodies present it also on their backs and shoulders Again, in all men the rudimentary hair on the upper and lower arm is directed towards the elbow—a peculiarity which occurs nowhere else in the animal kingdom, with the exception of the anthropoid apes and a few American monkeys, where it presumably has to do with arboreal habits For, when sitting in trees, the orang, as observed by Mr Wallace, places its hands above its head with its elbows pointing downwards, the disposition of hair on the arms and fore-arms then has the effect of thatch in turning the rain Again, I find that in all species of apes, monkeys, and baboons which I have examined (and they have been numerous), the hair on the backs of the hands and feet is continued as far as the first row of phalanges, but becomes scanty, or disappears altogether, on the second row, while it is invariably absent on the terminal row I also find that the same peculiarity occurs in man We all have rudimentary hair on the first row of phalanges, both of hands and feet when present at all, it is more scanty on the second row, and in no case have I been able to find any on the terminal row In all cases these peculiarities are congenital, and the total absence or partial presence of hair on the second phalanges is constant in different species of Quadrumana For instance it is entirely absent in all the chimpanzees, which I have examined while scantily present in all the orangs As in man, it occurs in a patch midway between the joints.

Besides showing these two features with regard to disposition of hair on the human arm and hand the woodcut on page 88 (Fig 22) illustrates a third By looking closely at the arm of the very hairy man from whom

the specimen of the latter however, from which the drawing was taken this characteristic was not well marked The downward direction of the hair on the backs of the hands is exactly the same in man as it is in all the anthropoid apes Again with regard to hair, Darwin notices that occasionally there appears in man a few hairs in the eye brows much longer than the others and that they seem to be

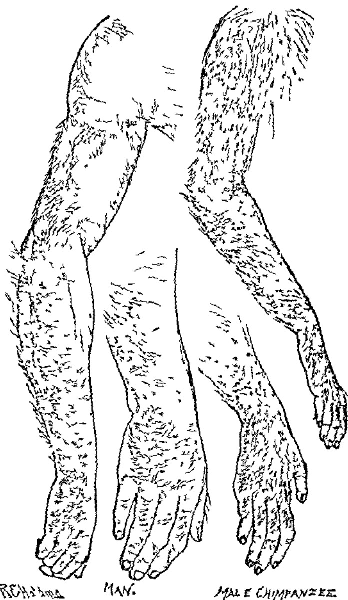


Fig 22 —Hair tracts on the arms and hands of man as compared with those of the chimpanzee Drawn from life (*From Romanes*)

representative of similarly long and scattered hairs which occur in the chimpanzee, macacus, and baboons

Lastly, it may be here more conveniently observed than in the next chapter on Embryology, that at about the sixth month the human foetus is often thickly coated with somewhat long dark hair over the entire body, except the soles of the feet and palms of the hands, which are likewise bare in all quadrumanous animals This covering, which is called the lanugo, and sometimes extends even to the whole forehead, ears, and face, is shed before birth So that it appears to be useless for any purpose other than that of emphatically declaring man a child of the monkey

9 Teeth —Darwin writes

"It appears as if the posterior molar or wisdom teeth were tending to become rudimentary in the more civilized races of man These teeth are rather smaller than the other molars, as is likewise the case with the corresponding teeth in the chimpanzee and orang, and they have only two separate fangs They are also much more liable to vary, both in structure and in the period of their development than the other teeth In the Melanian races, on the other hand, the wisdom teeth are usually furnished with three separate fangs, and are usually sound (i e not specially liable to decay), they also differ from the other molars in size, less than in the Caucasian races "

Now, in addition to these there are other respects in which the dwindling condition of wisdom teeth is manifested—particularly with regard to the pattern of their crowns Indeed, in this respect it would seem that even in the anthropoid apes there is the beginning of a tendency to degeneration of the molar teeth from behind forwards For if we compare the three molars in the lower jaw of the gorilla orang, and chimpanzee, we find that the gorilla has five well marked cusps on all three of them, but that in the orang the cusps are not so pronounced, while in the chimpanzee there are only four of them on the third molar Now in man it is only the first of these three teeth which normally presents five cusps, both the others presenting only four So that, comparing all these genera together, it appears that the number of cusps is being reduced from behind forwards, the chimpanzee having lost one of them from the third molar, while man has *not only lost this, but also one from the second molar,—and it* may be added likewise partially (or even totally) from the first molar, as a frequent variation among civilized races But, on the other hand variations are often met with in the opposite direction where the

second or the third molar of man presents five cusps—in the one case following the chimpanzee in the other the gorilla These latter variations, therefore, may fairly be regarded as reversionary For these facts I am indebted to the kindness of Mr C S Tomes

10 Perforations of the humerus —The peculiarities which we have to notice under this heading are two in number First, the supra condyloid foramen is a normal feature in some of the lower Quadrumana (Fig 24), where it gives passage to the great nerve of

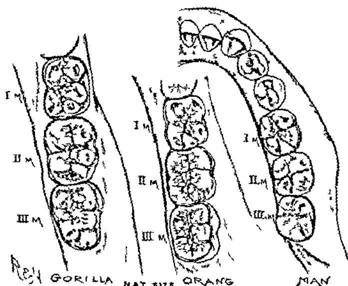


Fig 23 —Molar teeth of lower jaw in gorilla orang and man Drawn from nature nat size (*From Romanes*)

the forearm and often also to the great artery In man, however, it is not a normal feature Yet it occurs in a small percentage of cases—viz, according to Sir W Turner, in about one per cent, and therefore is regarded by Darwin as a vestigial character Secondly, there is inter-condyloid foramen, which is also situated near the lower end of the humerus, but more in the middle of the bone This occurs, but not constantly, in apes, and also in the human species. From the fact that it does so much more frequently in the bones of ancient —and also of some savage—races of mankind (viz in 20 to 30 per cent of cases), Darwin is disposed to regard it also as a vestigial feature.

On the other hand, Prof Flower tells me that in his opinion it is but an expression of impoverished nutrition during the growth of the bone

11 Flattening of Tibia —In some very ancient human skeletons there has also been found a lateral flattening of the tibia which rarely occurs in any existing human beings but which appears to have been usual among the earliest races of mankind hitherto discovered According to Broca, the measurements of these fossil human tibiae resemble those of apes Moreover, the bone is bent and strongly

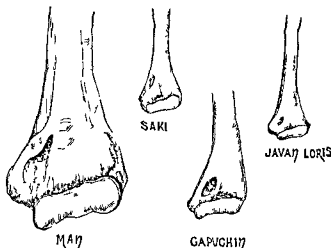


FIG 24.—Perforat ons of the humerus (supra condyloid forame) in three spec es of Quadrumana where it normally o curs and in man where it does not normally o cur Drawn from nature (*From Romanes*)

convex forwards while its angles are so rounded as to present the nearly oval section seen in apes It is in association with these ape like human tibiae that perforated humeri of man are found in greatest abundance

On the other hand however there is reason to doubt whether this form of tibia in man is really a survival from his quadrumanous ancestry For as Boyd Dawkins and Hartmann have pointed out the degree of flattening presented by some of these ancient human bones *is greater than that which occurs in any existing species of* anthropoid ape Of course the possibility remains that the unknown species of ape from which man descended may have had its tibia more flattered than is now observable in any of the existing species Never

theless, as some doubt attaches to this particular case, I do not press it—and, indeed, only mention it at all in order that the doubt may be expressed

Similarly, I will conclude by remarking that several other instances of the survival of vestigial structures in man have been alleged, which are of a still more doubtful character Of such, for example, are the supposed absence of the genial tubercle in the case of a very ancient jaw-bone of man, and the disposition of valves in human veins From the former it was argued that the possessor of this very ancient jaw bone was probably speechless inasmuch as the tubercle in existing man gives attachment to muscles of the tongue From the latter it has been argued that all the valves in the veins of the human body have reference, in their disposition to the incidence of blood pressure when the attitude of the body is horizontal, or quadrupedal Now, the former case has already broken down, and I find that the latter does not hold But we can well afford to lose such doubtful and spurious cases in view of all the foregoing unquestionable and genuine cases of vestigial structures which are to be met with even within the limits of our own organization—and even when these limits are still further limited by selecting only those instances which refer to the very latest chapter of our long ancestral history

CHAPTER VI

EVIDENCES FROM CLASSIFICATION

THE PRINCIPLES OF CLASSIFICATION[1]

A F SHULL

The International Code —Some of the essential features of the International Code are as follows The first name proposed for a genus or species prevails on the condition that it was published and accompanied by an adequate description definition or indication, and that the author has applied the principles of binomial nomenclature This is the so-called *law of priority* The tenth edition of the *Sytema Naturae* of Linnaeus is the basis of the nomenclature The author of a genus or species is the person who first publishes the same in connection with a definition indication or description and his name in full or abbreviated is given with the name thus *Bascanian anthonyi* Stejneger In citations the generic name of an animal is written with a capital letter, the specific and subspecific name without initial capital letter The name of the author follows the specific name (or subspecific name if there is one) without intervening punctuation If a species is transferred to a genus other than the one under which it was first described or if the name of a genus is changed the author s name is included in parentheses For example *Bascanion anthonyi* Stejneger should now be written *Coluber anthonyi* (Stejneger) the generic name of this snake having been changed One species constitutes the *type* of the genus that is it is formally designated as typical of the genus One genus constitutes the type of the subfamily (when a subfamily exists), and one genus forms the type of the family The type is indicated by the describer or if not indicated by him is fixed by another author The name of a subfamily is formed by adding the ending *-inae* and the name of a family by adding *-idae* to the root of the name of the type genus For example Colubrinae and Colubridae are the subfamily and family of snakes of which Coluber is the type genus

The basis of classification —Early systematists largely employed superficial characters to differentiate and classify animals and their

[1] From A. F Shull *Principles of Animal Biology* (copyright 1920) Used by special permission of The McGraw Hill Book Company

classifications were thus largely artificial and served principally as convenient methods of arrangement, description and cataloging Since the time of the development of the theory of descent with modifications by Lamarck (1809) and Darwin (1859), there has been an attempt to base the classification on relationships Very nearly related animals are put into the same species They are related because they descend from a common ancestry, and that common ancestry could not in most cases have been very ancient, otherwise evolution within the group would have occurred and the species would have been split into two or more species Species that are much alike are included in one genus being thus marked off from the species of another genus The similarity of the species of a genus is held to indicate kinship but since there is greater diversity among the individuals of a genus than among the members of a species, the common stock from which the species of a genus have sprung must have existed at an earlier time in order that evolution could bring about the degree of divergence now observed In like manner, a family is made up of genera, and their likeness is again a sign of affinity But to account for the greater difference between the extreme individuals belonging to a family evolution must have had more time that is, the common source of the members of a family must have antedated the common source of the individuals of a genus Orders classes, and phyla are similarly regarded as having sprung from successively more remote ancestors the time differences being necessary to allow for the differences in the amount of evolution This statement is in general correct However, since evolution has probably not proceeded at the same rate at all periods nor in all branches of the animal kingdom at any one time, the time relations of the groups of high or low rank must not be too rigidly assigned Thus certain genera, in which evolution has been slow, are probably much older than some families in which evolution has been rapid It is not improbable also that some genera are quite as old as the families which include them, but in no case can they be older Furthermore, different groups are classified by taxonomists of different temperaments so that groups of a given nominal rank may be much more inclusive (and hence older) in one branch of the animal kingdom than in another On the whole, nevertheless, the groups of higher rank have sprung from ancestry more remote than that of the groups of lower rank

The means of recognizing the kinship implied in classification permit some differences of opinion It is recognized that likeness in

structural characters is the chief clue to affinities. However, the evidential value of similarity in one or several structures unaccompanied by the similarity of all parts is to be distrusted, since animals widely separated and dissimilar in most characters may have certain other features in common Thus, the coots, phalaropes and grebes among birds have lobate feet but, as indicated by other features, they are not closely related, and there are certain lizards (Amphisbaenidae) which closely resemble certain snakes (Typholopidae) in being blind, limbless, and having a short tail The early systematists were very liable to bring together in their classification analogous forms that is, those which are functionally similar, or animals which are superficially similar In contrast with the early practice, the aim of taxonomists at the present time is to group forms according to homology, which is considered an indication of actual relationship Since a genetic classification must take into consideration the entire animal the search for affinities becomes an attempt to evaluate the results of all morphological knowledge, and it is also becoming evident that other things besides structure may throw light upon relationships The fossil records geographical distribution, ecology and experimental breeding may all assist in establishing affinities

The method of taxonomy—It is evident that before the relationships of animals can be determined the forms must be known, for unknown forms constitute breaks in the pedigrees of the groups to which they belong Moreover as pointed out above, the structural characters, variation and distribution must be known before a form can be placed in the proper place in a genetic system For these reasons an important part of systematic work is the description of forms and an analysis of their differences After the Linnaean system was adopted zoologists attacked this virgin field and for many years "species making' predominated Even at the present time when other aspects of zoology have come to receive relatively more attention it is an interesting fact that the analytical method prevails in systematic studies, and taxonomy suffers from and in part merits the criticism that it is a mere cataloging of forms and ignores the higher goal of investigation, namely, the discovery of the course of evolution Many systematists however, recognize that the ultimate purpose of taxonomic work is to discover the relationships as well as the differences between the described forms in order that the course of evolution may be determined In other words, it is appreciated that while analytical studies are necessary they are only preliminary, and

that upon their results must be built synthetic studies, if taxonomy is to fulfil its purpose

THE METHOD OF CLASSIFICATION

CHARLES DARWIN[1]

Naturalists, as we have seen, try to arrange the species, genera, and families in each class on what is called the Natural System But what is meant by this system? Some authors look at it merely as a scheme for arranging together those living objects which are most alike, and for separating those which are most unlike, or as an artificial method of enunciating, as briefly as possible, general propositions,—that is, by one sentence to give the characters common, for instance to all mammals, by another those common to all carnivora, by another those common to the dog genus, and then, by adding a single sentence, a full description is given of each kind of dog The ingenuity and utility of this system are indisputable But many naturalists think that something more is meant by the Natural System, they believe that it reveals the plan of the Creator, but unless it be specified whether order in time or space, or both, or what else is meant by the plan of the Creator, it seems to me that nothing is thus added to our knowledge Expressions such as that famous one by Linnaeus, which we often meet with in a more or less concealed form, namely, that the characters do not make the genus, but that the genus gives the characters, seem to imply that some deeper bond is included in our classifications than mere resemblance I believe that this is the case, and that community of descent—the one known cause of close similarity in organic beings—is the bond which, though observed by various degrees of modification is partially revealed to us by our classifications

Let us now consider the rules followed in classification, and the difficulties which are encountered on the view that classification either gives some unknown plan of creation, or is simply a scheme for enunciating general propositions and of placing together the forms most like each other It might have been thought (and was in ancient times thought) that those parts of the structure which determined the habits of life, and the general place of each being in the economy of nature, would be of very high importance in classification Nothing can be more false No one regards the external similarity of a mouse to a shrew, of a dugong to a whale, of a whale to a fish, as of any

[1] From *The Origin of Species*

importance These resemblances, though so intimately connected with the whole life of the being, are ranked as merely 'adaptive or analogical characters' but to the consideration of these resemblances we shall recur It may even be given, as a general rule that the less any part of the organisation is concerned with special habits the more important it becomes for classification As an instance Owen, in speaking of the dugong, says, 'The generative organs, being those which are most remotely related to the habits and food of an animal I have always regarded as affording very clear indications of its true affinities We are least likely in the modifications of these organs to mistake a merely adaptive for an essential character With plants how remarkable it is that the organs of vegetation, on which their nutrition and life depend, are of little signification whereas the organs of reproduction, with their product the seed and embryo are of paramount importance[1] So again in formerly discussing certain morphological characters which are not functionally important, we have seen that they are often of the highest service in classification This depends on their constancy throughout many allied groups and their constancy chiefly depends on any slight deviations not having been preserved and accumulated by natural selection which acts only on serviceable characters

WHAT IS A SPECIES?

Each kind of animal or plant that is each set of forms which in the changes of the ages has diverged tangibly from its neighbors is called a species There is no absolute definition for the word species The word kind represents it exactly in common language, and is just as susceptible to exact definition The scientific idea of species does not differ materially from the popular notion A kind of tree or bird or squirrel is a species Those individuals which agree very closely in structure and function belong to the same species There is no absolute test, other than the common judgment of men competent to decide Naturalists recognize certain formal rules as assisting in such a decision A series of fully intergrading forms however varied at the extremes, is usually regarded as forming a single species There are certain recognized effects of climate of climatic isolation, and of the isolation of domestication These do not usually make it necessary to regard as distinct species the extreme forms of a series concerned [1]

[1] From D S Jordan and V L Kellogg *Evolution and Animal Life*

The term 'species was thus defined by the celebrated botanist De Candolle 'A species is a collection of all the individuals which resemble each other more than they resemble anything else, which can by mutual fecundation produce fertile individuals and which reproduce themselves by generation in such a manner that we may from analogy suppose them all to have sprung from one single individual And the zoologist Swainson gives a somewhat similar definition A species in the usual acceptation of the term is an animal which, in a state of nature is distinguished by certain peculiarities of form, size colour or other circumstances from another animal It propagates after its kind individuals perfectly resembling the parent its peculiarities therefore are permanent [1]

As will have become apparent, the significant assumption underlying classification is that the closest fundamental similarities between animals (or plants) are found in the forms most closely related and that the greatest differences are found in those forms which are unrelated or at best very distantly related The assumption implies the idea of descent with modification which is no more nor less than evolution Using this evolutionary basis we can arrive at an extremely satisfactory classification both of living and of extinct forms and there is no other basis of classification that works

The question might well be asked whether it is possible to test the validity of the assumption that degrees of resemblance vary directly with closeness of blood relationship? Two direct tests of this may be and have been made The closest of blood relatives possible are individuals that have been derived by the dividing of a single egg Armadillo[2] quadruplets have been shown to be thus derived, and detailed studies of the closeness of resemblance existing between members of a given set indicate that they are vastly more alike than are the simultaneously born offspring of animals which give birth to several young, but in which each young is derived from a separate egg If we use the index of correlation to indicate the degree of similarity between individuals we find that ordinary brothers or sisters are only about 50 per cent alike, while armadillo quadruplets are over 90 per cent alike Identical or duplicate twins in human beings are believed to have an origin from one egg, after the fashion of the armadillo

[1] From A R Wallace *Darwinism*

[2] See H H Newman *The Biology of Twins* (1917) University of Chicago Press

though the proof has not been forthcoming Everyone is familiar with the remarkable similarity, amounting almost to identity, between such twins Thus we are able to show that the closest blood relationship known is associated with the closest resemblance The next degree of resemblance is between members of the same family brothers sisters, cousins, etc., and we do not hesitate to explain this resemblance as due to blood relationship In this we merely accept the known principles of heredity

The second direct test of the validity of the assumption that degrees of resemblance run parallel with degrees of blood relationship is found in connection with "blood precipitation tests" This evidence, as presented by Professor Scott forms the substance of the next chapter

obtained with the bloods of Simiidae (i e Man like Apes) closely resemble those obtained with human blood the bloods of Cercopithecidae (Old World Monkeys) came next followed by those of Cebidae and Hapal dae (New World Monkeys and Marmosets) which gave but slight reactions with anti human serum whilst the blood of Lemuroidea gave no indication of blood relationship A perusal of the pages relating to the tests made upon the many bloods I have examined by means of prec p tating anti sera will very clearly show that this method of investigation permits of our drawing certain definite conclusions It is a remarkable fact that a common property has persisted in the bloods of certain groups of animals throughout the ages wh ch have elapsed during their evolution from a common ancestor and this in spite of differences of food and habits of life The persistence of the chemical blood relationship between the various groups of animals serves to carry us back into geological times and I believe we have but begun the work along these lines and that it will lead to valuable results in the study of various problems of evolution

The general conclusions on interrelationships so far as they are of particular interest for our purpose reached by Nuttall and Graham Smith as the result of many thousands of blood tests may be summarized as follows

1 If sufficiently strong solutions be used and time enough be allowed a relationship between the bloods of all mammals is made evident

2 The degrees of relationship between man apes and monkeys have already been noted.

3 Anti-carnivore sera show a preponderance of large reactions amongst the bloods of Carnivora as distinguished from other Mammalia the maximum reactions usually take place amongst the more closely related forms in the sense of descriptive zoölogy

4 Anti pig serum gives maximum reactions only with the bloods of other species of the same family moderate reactions those of ruminants and camels and moderate or slight reactions with those of whales Anti llama serum gives a moderate reaction with the blood of the camel and the close relationship between the deer family and the *great host of antelopes sheep goats and oxen is clearly demonstrated*

5 Anti whale serum gives maximum reactions only with the bloods of other whales and slight reactions with those of pigs and ruminants.

6 A close relationship is shown to exist between all marsupials *with the exception of the Thylacine, or so-called Tasmanian Wolf*

7 Strong anti turtle serum gives maximum reactions only with the bloods of turtles and crocodiles, with those of lizards and snakes the results are almost negative With the egg albumins of reptiles and birds a moderate reaction is given

8 Anti lizard serum produces maximum results with the bloods of lizards and reacts well with those of snakes

9 These experiments indicate that there is a close relationship between lizards and snakes, on the one hand, turtles and crocodiles on the other They further indicate that birds are more nearly allied with the turtle crocodile series than with the lizard snake series results for which palaeontological studies had already prepared us

10 "Tests were made by means of anti sera for the fowl and ostrich upon 792 and 649 bloods respectively They demonstrate a similarity in blood constitution of all birds, which was in sharp contrast to what had been observed with mammalian bloods, when acted upon by anti mammalian sera Differences in the degree of reaction were observed, but did not permit of drawing any conclusions"

11 I have already called attention to the fact that the problematical Horseshoe crab is indicated by its embryology to be related to the air breathing spiders and scorpions rather than to the marine Crustacea It is of exceptional interest to learn that embryology is supported by the results of the blood tests

It must not be supposed that there is any exact mathematical ratio between the degrees of relationship indicated by the blood tests and those which are shown by anatomical and palaeontological evidence Any supposition of the kind would be immediately negatived by the contrast between the blood of mammals and that of birds It could hardly be maintained that an ostrich and a parrot are more nearly allied than a wolf and a hyena and yet that would be the inference from the blood tests Like all other anatomical and physiological characters the chemical composition of the blood is subject to change in the course of evolution and these developmental changes do not keep equal pace in all parts of the organism It is the rule rather than the exception to find that one part of the structure advances much more rapidly than other parts, such as the teeth, the skull, or the feet The human body is, fortunately for us, of rather a primitive kind while the development of the brain is far superior to that of any other mammal and this great brain development has

necessitated a remodeling of the skull On the other hand, the skeleton, limbs, hands and feet are but slightly specialized In the elephant tribe, so far as we can trace them back in time, there has been little change, save in size, in the structure of the body or limbs, while the teeth and skull have passed through a series of remarkable changes It is for this reason that it is unsafe to found a scheme of classification, which is meant to be a brief expression of relationship, upon a single character, for the result is almost invariably misleading The results of blood tests must be critically examined and checked by a comparison with the results obtained by other methods of investigation, but after every allowance has been made, these tests are very remarkable

The blood tests have brought very strong confirmation to the theory of evolution and from an entirely unexpected quarter, they come as near to giving a definite demonstration of the theory as we are likely to find, until experimental zoology and botany shall have been improved and perfected far beyond their present state.

CHAPTER VIII

EVIDENCES FROM EMBRYOLOGY

THE FACTS OF REPRODUCTION AND DEVELOPMENT

It is now definitely known that all living creatures are mortal, at least as individuals, but they all have the capacity of continuing their life by the reproduction of offspring This physical immortality is based upon an actual transmission from parent to offspring of some material substance which is so organized chemically as to be fully representative of the race or stock to which the parent belongs

Reproduction may be *asexual* or *sexual* In *asexual development* a new individual may be produced by a process of *fission* (dividing the parent into two or more parts, each of which has the capacity to develop into a whole new individual), by *budding* (the production of new individuals by means of outgrowths of the parent body), or by giving off spores or eggs capable of development without fertilization (*parthenogenesis*) In *sexual reproduction* two kinds of parent individuals exist one a female which is capable of giving off relatively large single cells called eggs (ova), and the other a male, which is capable of producing minute, usually motile cells, called spermatozoa A union of ovum and spermatozoon is usually necessary before the ovum can begin its development It is the sexual method of reproduction that will chiefly concern us here, and, for present purposes, we may omit any further mention of the various asexual methods

An ovum may be conceived of as an individual of some definite species or race reduced to the very lowest terms It exhibits the characteristic cell structure, consisting of cytoplasm and nucleus cell membrane, nuclear membrane, usually a centrosome (Fig 40) Further details as to the minute structure of the nucleus are given in chapter xliv, where the mechanism of Mendelian heredity is dealt with

' The reproductive cells from the two sexes,' says Wright,[1] "have very different appearances In mammals the ovum is a relatively large, spherical cell, just visible to the naked eye

[1] From Sewall Wright *Principles of Livestock Breeding* United States Department of Agriculture Bulletin No 905

"In birds, the yolk of an egg is really a single ovum, distended to an enormous size by food material The sperm cell is very much smaller and can be seen well only with a high power microscope It is something like a tadpole in shape, having a small cell body, containing a little nucleus, and attached to this a long, whiplike process which beats rapidly while the cell is alive, enabling it to seek out and unite with the large passive egg in the act of fertilization Enormous numbers of sperm cells are produced by the male, but only one takes part in fertilization After the first has penetrated the membrane of an egg cell, a change takes place in the latter which prevents the entrance of others

"The sperm activates certain formerly inert substances in the egg and the new combination cell (the *zygote*) starts almost at once to produce a new individual'

OUTLINE OF ANIMAL DEVELOPMENT[1]

D S JORDAN AND V I KELLOGG

The embryonic development is from the beginning up to a certain point practically alike looked at in its larger aspect, for all the many celled animals That is there are certain principal or constant characteristics of the beginning development which are present in the development of all many celled animals The first stage or phenomenon of development is the simple fission of the germ cell into halves (Fig 25, *b*) These two daughter cells next divide so that there are four cells (*c*), each of these divides, and this division is repeated until a greater or lesser number (varying with the various species or groups of animals) of cells is produced These cells may not all be of the same size, but in many cases they are, no structural differentiation whatever being apparent among them

The phenomenon of repeated division of the germ cell is called cleavage, and this cleavage is the first stage of development in the case of all many-celled animals The germ or embryo in some animals consists now of a mass of few or many undifferentiated primitive cells lying together and usually forming a sphere (Fig 25 *e*), or perhaps separated and scattered through the food yolk of the egg The next stage of development is this the cleavage cells arrange themselves so as to form a usually hollow sphere or ball, the cells lying side by side to

[1] From D S Jordan and V L Kellogg *Evolution and Animal Life* (copyright 1907) Used by special permission of the publishers D Appleton & Company

form the outer circumferential wall of this hollow sphere (*f*) This is called the *blastula* or *blastoderm* stage of development, and the embryo itself is called the blastula or blastoderm This stage also is common to all the many celled animals The next stage in embryonic develop ment is formed by the bending inward of a part of the blastoderm cell layer, as shown in (*g*) (or the splitting off inwardly of cells from a special part of the blastula cell layer) This bending in may produce a small depression or groove, but whatever the shape or extent of the sunken in part of the blastoderm, it results in distinguishing the blastoderm layer into two parts, a sunken in or inner portion called

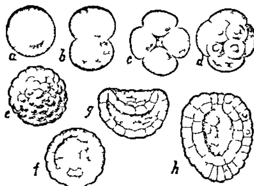


FIG 25 —First stages in the embryonic development of the pond snail *Lymnaeus* *a* egg cell *b* first cleavage *c* second cleavage *d* third cleavage *e* after numerous cleavages *f* blastula—in section *g* gastrula just forming—in section *h* gastrula completed—in section (*From Jordan and Kellogg after Rabl*)

the *endoblast* and the other unmodified portion called the *ectoblast* *Endo* means within and the cells of the endoblast often push so far into the original blastoderm cavity as to come into contact with the cells of the ectoblast and thus obliterate this cavity (*h*) This third well marked stage in the embryonic development is called the *gastrula* stage, and it also occurs in the development of all or nearly all many celled animals

In the case of a few of the simple many celled animals the embryo hatches—that is, issues from the egg at the time of or very soon after reaching the gastrula stage In the higher animals however, develop ment goes on within the egg or within the body of the mother until the embryo becomes a complex body, composed of many various

tissues and organs Almost all the development may take place within the egg, so that when the young animal hatches there is necessary little more than a rapid growth and increase of size to make it a fully developed mature animal This is the case with the birds, a chicken just hatched has most of the tissues and organs of a full grown fowl and is simply a little hen But in the case of other animals the young hatches from the egg before it has reached such an advanced stage of development, a young starfish or young crab or young honeybee just hatched looks very different from its parent It has yet a great deal of development to undergo before it reaches the structural condition of a fully developed and fully grown starfish or crab or bee Thus *the development of some animals is almost wholly embryonic develop* ment—that is, development within the egg or in the body of the mother—while the development of other animals is largely post embryonic, or larval development, as it is often called There is no important difference between embryonic and postembryonic develop ment. The development is continuous from egg cell to mature animal and whether inside or outside of an egg it goes on regularly and uninter ruptedly

The cells which compose the embryo in the cleavage stage and blastoderm stage and even in the gastrula stage, are apparently all similar, there is little or no differentiation shown among them But from the gastrula stage on, development includes three important things the gradual differentiation of cells into various kinds to form the various kinds of animal tissues the arrangement and grouping of these cells into organs and body parts, and finally the developing of *these organs and body parts into the special condition characteristic* of the species of animal to which the developing individual belongs From the primitive undifferentiated cells of the blastoderm, development leads to the special cell types of muscle tissue, of bone tissue of nerve tissue, and from the generalized condition of the embryo in its early stages, development leads to the specialized condition of the body of the adult animal Development is from the general to the special, as was said years ago by von Baer, the first great student of development

A starfish, a beetle, a dove and a horse are all alike in their beginning—that is, the body of each is composed of a single cell a *single structural unit And they are all alike, or very much alike* through several stages of development, the body of each is first a single cell then a number of similar undifferentiated cells, and then a

blastoderm consisting of a single layer of similar undifferentiated cells But soon in the course of development the embryos begin to differ, and as the young animals get further and further along in the course of their development, they become more and more different until each finally reaches its fully developed mature form, showing all the great structural differences between the starfish and the dove, the beetle and the horse That is, all animals begin development apparently alike but gradually diverge from each other during the course of development

There are some extremely interesting and significant things about this divergence to which attention should be given While all animals are apparently alike structurally at the beginning of development, so far as we can see, they do not all differ noticeably at the time of the first divergence in development The first divergence in development is to be noted between two kinds of animals which belong to different great groups or classes But two animals of different kinds, both belonging to some one great group, do not show differences until later in their development This can best be understood by an example All the butterflies and beetles and grasshoppers and flies belong to the great group or class of animals called Insecta, or insects There are many different kinds of insects, and these kinds can be arranged in subordinate groups (orders), such as the Diptera, or flies, the Lepidoptera, or butterflies and moths, and so on But all have certain structural characteristics in common, so that they are comprised in one great class—the Insecta Another great group of animals is known as the Vertebrata, or backboned animals The class Vertebrata includes the fishes, the batrachians, the reptiles, the birds and the mammals, each composing a subordinate group, but all characterized by the possession of a backbone or, more accurately speaking, of a notochord, a backbonelike structure Now, an insect and a vertebrate diverge very soon in their development from each other, but two insects, such as a beetle and a honeybee, or any two vertebrates, such as a frog and a pigeon, do not diverge from each other so soon That is all vertebrate animals diverge in one direction from the other great groups, but all the members of the great group keep together for some time longer Then the subordinate groups of the Vertebrata, such as the fishes, the birds, and the others, diverge, and still later the different kinds of animals in each of these groups diverge from each other

That the course of development of any animal from its beginning to fully developed adult form is—in all its essentials—fixed and certain

is readily seen All rabbits develop in the same way every grasshopper goes through the same developmental changes from single egg cell to the full grown active hopper as every other grasshopper of the same kind—that is development takes place according to certain natural laws the laws of animal development These laws may be roughly stated as follows All many celled animals begin life as a single cell the fertilized egg cell each animal goes through a certain orderly series of developmental changes which accompanied by growth leads the animal to change from a s ngle cell to the many celled complex form characteristic of the species to which the animal belongs this development is from simple to complex structural condition the development is the same for all individuals of one species While all animals begin development similarly the course of development in the different groups soon diverges the divergence being of the nature of a branching like that shown in the growth of a tree In the free tips of the smallest branches we have represented the various species of animals in their fully developed condition all standing more or less clearly apart from each other But in tracing back the development of any kind of animal we soon come to a point where it very much resembles or becomes apparently identical with the development of some other kind of animal and in addition the stages passed through n the developmental course may very much resemble the fully developed mature stages of lower animals To be sure any animal at any stage in its existence differs absolutely from any other kind of animal in that it can develop into only its own kind of animal There is something inherent in each developing animal that gives it an identity of its own Although in its young stages it may be hardly distinguishable from some other kind of animal in similar stages it is sure to come out when fully developed an individual of the same kind as its parents were or are. A very young fish and a very young salamander are almost indistinguishably alike but one is sure to develop into a fish and the other into a salamander This certainty of an embryo to become an individual of a certain kind is called the law of heredity Viewed in the light of development there must be as great a difference between one egg and another as between one animal and another for the greater difference is included in the less

The significance of the developmental phenomena is a matter about which naturalists have yet very much to learn It is believed however by practically all naturalists that many of the various stages in the development of an animal correspond to or repeat in ma

fundamental features at least, the structural condition of the animal's ancestors Naturalists believe that all backboned or vertebrate

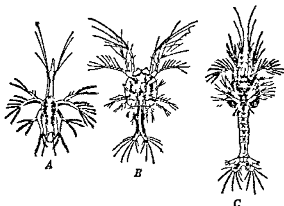


FIG 26 —Stages in the development of the prawn, *Peneus potimirium* *A* Nauplius larva, *B*, first zoea stage, *C*, second zoea stage (*From Jordan and Kellogg, after Fritz Muller*)

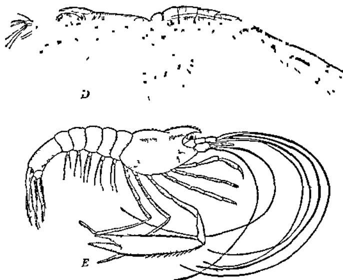


FIG 27 —Later stages in the development of the prawn, *Peneus potimirium* *D*, Mysis stage, *E*, adult stage (*From Jordan and Kellogg*)

animals are related to each other through being descended from a common ancestor, the first or oldest backboned animal In fact, it is because all these backboned animals—the fishes, the batrachians, the reptiles, the birds and the mammals—have descended from a common ancestor that they all have a backbone It is believed that the descendants of the first backboned animal have in the course of many generations branched off little by little from the original type until there came to exist very real and obvious differences among the backboned animals—differences which among the living backboned animals are familiar to all of us *The course of development of an individual animal is believed to be a very rapid and evidently much condensed and changed recapitulation of the history which the species or kind of animal to which the developing individual belongs has passed through in the course of its descent through a long series of gradually changing ancestors* If this is true then we can readily understand why a fish and a salamander a tortoise, a bird and a rabbit, are all much alike, as they really are, in their earlier stages of development, and gradually come to differ more and more as they pass through later and later developmental stages. A crab has a tail in one of its developmental stages, so that at that time it looks like and really is like the mature stage of some tailed crustacean like a crayfish A barnacle, which looks little like a crayfish or crab in its mature stage, is hardly to be distinguished in its immature life from a young crab or lobster Sacculina, which is a still more degenerate crustacean, is only a sort of feeding sac with rootlet like processes projecting into the body of the host crab on which it lives as a parasite, but the young free swimming Sacculina is essentially like a barnacle, crayfish, or crab in its young stage.

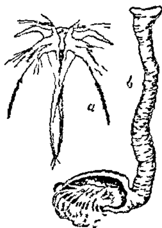


Fig 28 —Metamorphosis of a barnacle *Lepas* *a* larva *b* adult. (*From Jordan and Kellogg*)

However, it is obvious that this recapitulation or repetition of ancestral stages is never perfect, and it is often so obscured and modified by interpolated adaptive stages and characters that but little of an animal s ancestry can be learned from a scrutiny of its development

The fascinating biogenetic law of Müller and Haeckel summed up in the phrase, "*ontogeny is a recapitulation of phylogeny*," must not be too heavily leaned on as a support for any speculations as to the phyletic affinities of any species or group of species of organisms "Embryology is an ancient manuscript with many of the sheets lost, others displaced, and with spurious passages interpolated by a later hand."

CHAPTER IX

CRITIQUE OF THE RECAPITULATION THEORY[1]

W B SCOTT

Embryology is the study of the development of the individual organism from its beginning in the egg to the attainment of the adult condition This individual development is called *ontogeny* and the question of the relation of ontogeny to the ancestral history of the species or *phylogeny* constitutes one of the main problems of embryology Around this problem many controversies have raged, controversies which have by no means arrived at a definite solution even to-day Thirty years ago the "recapitulation theory" was well nigh universally accepted, according to which the individual development, or ontogeny, was regarded as an abbreviated repetition of the ancestral history of the species, or phylogeny Haeckel called this theory the "fundamental biogenetic law" and upon it he established his whole "History of Creation" Nowadays, that "fundamental law" is very seriously questioned and by some high authorities is altogether denied However, even those who take this extreme position concerning the recapitulation theory see in the facts of embryology one of the strongest supports of the doctrine of evolution

It was very early recognized that the recapitulation theory could not be applied with literal exactness, but was subject to certain important exceptions and qualifications.

1 That the history must have been enormously abbreviated After three weeks of incubation the tiny speck of protoplasm, which forms a circular mark on the yolk of a hen's egg, is developed into a fully formed chick, ready for hatching and able in large degree to take care of itself On the other hand, the evolution of birds from their invertebrate ancestors, through the fishes, amphibians, and reptiles, the separation of the gallinaceous stock from other birds and the differentiation of this particular species were extremely slow processes extending through unnumbered millions of years Admitting recapitulation to the fullest extent, it is evidently a physical impossibility

[1] From W B Scott *The Theory of Evolution* (copyright 1917) Used by special permission of the publishers, The Macmillan Company

that it should be a perfect repetition of phylogeny, very much of the long story must of necessity be omitted

2 Through all the stages of development the embryo must be rendered able to live and grow and thrive through adaptation to its surroundings and changes in its environment In some animals development takes place within the body of the mother, in others the embryo is protected by the hard egg shell, as in birds, while the eggs of certain fishes and many invertebrates float freely in the sea and are almost without protection Such differences in environment necessitate differences in the mode of development, while the presence or absence of a large amount of inert food material, or yolk exerts a great influence in determining the steps of ontogeny

3 Many animals pass through a larval stage of development, in which the immature young leads an independent and self sustaining existence, during which it is very different in appearance and structure from its adult parents Familiar instances of this mode of development are to be found in the tadpole which is the larva of the frog, and the caterpillar, the larva of a butterfly Larvae are fully subject to the struggle for existence and must adapt themselves to their environment and to changes in that environment exactly as do adults, if they are to survive In this way many changes are introduced into the ontogeny which can have no phylogenetic significance It is found in several known instances, that nearly allied species, living under different conditions, have quite different modes of ontogeny, though their ancestral history must have been substantially identical In one and the same species of marine worms for example, which inhabits both the warm Mediterranean and the cold waters of the North Sea the larva of the northern form is quite distinct from that of the southern In attempting to interpret the meaning of embryological facts, it is thus necessary to distinguish sharply between those features which are derived from a long inheritance, and are therefore called *palingenetic*, from those which have been secondarily introduced in response to the changing needs of embryonic or larval life These secondary features are termed *cenogenetic*

"If we are compelled to admit that cenogenetic characters are intermingled

pure source

accordingly

scope for its dangerous play, but in which positive results are by no means everywhere to be obtained To attain such results, the palin

genetic and cenogenetic phenomena must be sifted apart, an operation which required more than one critical grain of salt On what grounds shall this critique be based? Assuredly not by way of a vicious circle on the ontogeny again, for if cenogenetic characters are present in one case, who will guarantee that a second case, used for a comparison with the first, does not likewise appear in cenogenetic disguise? If it once be admitted that not everything in development is palingenetic, that not every ontogenetic fact can be accepted at its face value, so to speak, it follows that nothing in ontogeny is immediately available for the critique of embryonic development The necessary critique must be drawn from another source

These remarks of Gegenbaur s were called forth by the state of wild speculation into which embryological work had fallen As there were no generally accepted canons of interpretation for the facts of embryological development different writers interpreted these facts in the most divergent and contradictory manner, resulting in a chaotic confusion which led to a strong reaction against the whole method, though there can be little doubt that this reaction has gone too far

' It must be evident to any candid observer, not only that the embryological method is open to criticism, but that the whole fabric of morphology, so far as it rests upon embryological evidence, stands in urgent need of reconstruction For twenty years embryological research has been largely dominated by the recapitulation theory, and unquestionably this theory has illuminated many dark places and has solved many a perplexing problem that without its aid might have remained a standing riddle to the pure anatomist But while fully recognizing the real and substantial fruits of that theory, we should not close our eyes to the undeniable fact that it, like many another fruit ful theory, has been pushed beyond its legitimate limits It is largely to an overweening confidence in the validity of the embryological evidence that we owe the vast number of the elaborate hypothetical phylogenies which confront the modern student in such bewildering confusion The inquiries of such a student regarding the origin of any of the great principal types of animals involve him in a labyrinth of speculation and hypothesis in which he seeks in vain for conclusions of even an approximate certainty

Many other equally vigorous and well deserved criticisms of the embryological method might be cited but it should be emphasized that these criticisms are all directed against the application of the method to the solution of definite and concrete problems of descent and

relationship None of them denies and many strongly affirm that embryology affords some of the strongest and most convincing evi dence in favor of the evolutionary theory

Let us examine some of this evidence To begin with it should be noted that in following out the ontogeny or individual develop ment, the observer witnesses the formation of something new not merely the enlargement and unfolding of a pre existing organism though the theory of *preformation* which was widely accepted in the eighteenth century looked upon ontogeny precisely in that way as the growth of a germ which was the miniature of the parent. Such a theory was possible only before the development of microscopic technique had enabled the observer to detect the actual successive steps of change The egg is a single cell with the nucleus and all the parts of other undifferentiated cells though it may be enormously enlarged by the presence of food yolk In the hen s egg this food yolk is quite inert and the activity of development is confined to the minute disc of protoplasm on the outside of the yolk while in the frog s egg the yolk is disseminated though not uniformly throughout the egg and in the mammalian egg which is microscopic in size there is no yolk It is a very remarkable fact that all of the vertebrated animals fishes amphibians reptiles birds and mammals however different their habits and modes of life have a mode of ontogeny which is of even more characteristically and unmistakably the same plan than is the type of their adult structure which was described in the last chapter The egg or the active portion of it divides in a definite and regular manner into a very large number of cells which arrange them selves in definite layers an outer and an inner and within these layers cell aggregates form incipient organs which step by step take on the adult condition Not only is the plan and type of development essentially similar throughout the whole phylum of the vertebrates but in accordance with the recapitulation theory many structural features wh ch are permanent in lower forms appear in the embryos of higher and more advanced types In the latter however these features ar^ transitory and in the course of development they either disappear or are so modified as to be very different sometimes unrecog nizable in the adults

At a certain stage of the ontogeny the embryo of a mammal has gill pouches like a fish the skeletal supports of the gill pouches the arteries and veins which supply them with blood the structure of the heart in short the entire plan of the circulatory system is fish like.

At a later stage most of the gill pouches have been obliterated but one is retained and converted into the Eustachian canal which connects the throat with the middle ear, inside of the ear drum Similarly, the embryological evidence shows that the lungs of air breathers have been derived from the swim bladder of fishes a conclusion which had already been reached by comparative anatomy, for in a remarkable

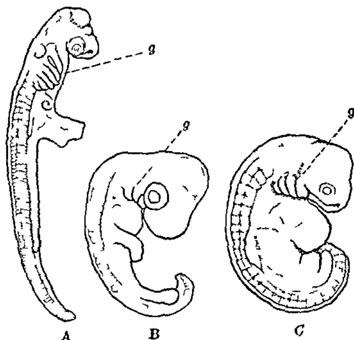


FIG 29 —Embryos in corresponding stage of development of shark (*A*) fowl (*B*) and man (*C*) g gill slits (*From Scott*)

group known as the Dipnoi or lung fishes, the air bladder is utilized for purposes of respiration

It has been objected that, while embryology may prove relationship within a single type, it fails to demonstrate any connection between different types but this is not altogether true The Tunicata a curious group of marine animals once referred to the Mollusca, are shown by their ontogeny to be related to the vertebrates and the same is true of certain marine worms (*Balanoglossus*) Indeed, most modern zoologists have adopted a scheme of classification, in which

the type Chordata includes not only the true vertebrates, but also the Lancelet (*Amphioxus*), the tunicates, and *Balanoglossus* this scheme is founded upon the embryological evidence Among the invertebrates even more remarkable examples have been observed Such radically different types as the segmented worms and the shell fish (Mollusca) are brought into relationship by their ontogeny and their closely similar types of larvae, as are also, though less distinctly the brachiopods or lamp shells and the Bryozoa The Horseshoe-crab, or King-crab, so abundant along our Atlantic coast, was long of uncertain affinities, originally referred to the Crustacea largely because of its marine habits of life, embryology makes much more probable its relationship to the air breathing scorpions and spiders, a result which has been examined previously from another point of view in connection with blood tests

Even before the publication of Darwin's *Origin of Species* one of the great stumbling blocks in the way of the theory of special creation was the existence in a great many animals of rudimentary organs or such as are so far reduced and atrophied as to be of no service to their possessors An analogy employed by my lamented friend Mr Richard Lydekker, may be advantageously repeated here Let us suppose that a screw steamer with longitudinal shaft leading aft from the engine room to the stern where it carries the propeller, should, on close examination, reveal many signs that it has originally been a ' side-wheeler, or paddle-boat Recognizable remnants of paddle boxes, of bearings for a transverse shaft, and the like are found what would be the inevitable conclusion? No one would maintain that a naval architect, in possession of his senses in constructing a screw steamer would deliberately introduce features which are useful and appropriate only in a paddle-boat The only reasonable explanation would be that the vessel had originally been built as a paddle-boat and had subsequently been converted into a screw steamer and in the conversion it had not been found necessary completely to eradicate all traces of the original construction Obviously the same reasoning applies to rudimentary organs The only satisfactory explanation of such useless remnants is that their possessors are descendants of ancestors in which those organs were fully functional It seems quite absurd to assume that in a separately and specially created animal useless structures reminiscent of other animals in which the same structures are useful and valuable should be included, merely to indicate ideal relationships and community of plan

It was sought to break the force of this very serious objection to the theory of special creation by saying that apparently useless organs may nevertheless have functions which are still unknown to us and may be revealed by future discovery In certain cases, like that of the thyroid gland in the neck, this contention has been justified, but there are many others to which it does not apply For example, in the great and varied whale tribe (order Cetacea) which includes the right, or whalebone whales, the sperm whales, the porpoises, dolphins, etc., the forelimbs have been converted into swimming paddles, but the hind limbs appear to have vanished completely, leaving no externally visible trace Internally, however, recognizable remnants of the hind limb bones may be found in various stages of reduction, which differ in the different members of the order In the Greenland Right Whale the hip-bone thigh bone and shin-bone are indicated, in the Finwhale only the hip bones and a minute rudiment of the thigh bone are to be found, in the toothed whales only an almost unrecognizable remnant of the hip bone is left and in one of the dolphins even that has disappeared Similarly, the snakes have lost their limbs completely, so far as external appearance is concerned, and in most members of the group no trace of limbs is to be found on dissection, but in certain snakes the rudiments of limbs are to be detected Leaving aside all preconceptions, which is the more probable explanation of such phenomena, the theory of special creation or the theory of evolution?

Even if it were admitted that all rudimentary organs and structures found in the adult have a certain unknown use and value, no one could maintain this with regard to the countless instances of structures which are developed in the embryo, but disappear entirely before birth It is possible to mention but a very few of such instances out of the great number that have already been observed and recorded, but these few will suffice to illustrate the principle involved

"Examples of this may be cited from the most widely different groups in the embryo of insects, especially of beetles, pairs of legs are formed within the egg, not only on the head and thorax, but also on the abdomen, but while those on the head are transformed into mouth parts those on the thorax are farther developed in their jointing and musculature to be locomotive legs, those on the abdomen are again resorbed In many fresh water worms, the eggs of which are laid in a cocoon, from which they are hatched as a finished, minute, crawling worm larval organs are nevertheless formed, which recall those of the Trochophore, the larva of the original worms, which swims

freely in the sea However, these larval organs are never properly functional, since no actually free swimming larva is developed but the embryo merely floats in the albuminous fluid of the cocoon

"A particularly beautiful example is offered by the whales in their embryological development, which has been thoroughly studied by Kukenthal In the adult condition they show only the anterior extremities, but in the embryo the posterior pair, with their skeletal parts, are formed, but are afterwards completely atrophied Although they are mammals, in the adult condition they have absolutely no covering of hair, since in their aquatic life another and more effective protection against loss of heat is given by means of a thick layer of blubber, only a few coarse bristles, partly with particular functions, have persisted on a few parts of the body But in the embryo a dense covering of hair is formed, which is later transformed in a peculiar manner and atrophied Further, a series of whales have no teeth in the adult condition, but only the well known eel-trap-like, horny plates, from which whale-bone is produced Nevertheless, in the embryo there is a dentition of numerous teeth, which are however resorbed, without ever piercing the gum"[1]

Throughout the great group of the ruminants which includes the oxen buffaloes, bison, sheep, goats, antelopes, deer and giraffes, the collar bone is invariably lacking since it is superfluous on account of the exclusively locomotive manner in which the fore legs are employed In the embryo sheep the collar bone is established and even to some extent ossified, but is subsequently resorbed and disappears entirely No doubt, the collar bone will be found in many other embryo ruminants, when the proper examination shall have been made, but its demonstrated presence in the foetal sheep is sufficiently striking In the higher mammals the number of teeth was originally 44, or 11 on each side of both upper and lower jaws, but in most of the modern or existing groups of these higher mammals this number has been very considerably reduced through the suppression of certain teeth We have every reason to believe that the ancestors of the forms with reduced dentition possessed teeth in full numbers and that there has actually been a loss of teeth in the course of descent This conclusion is abundantly confirmed by the facts of embryology Take, for example, the great group of the gnawing mammals or Rodentia, in which the front teeth or incisors, above and below, are reduced to one on each side, except in the rabbits The incisors are chisel shaped and

[1] Otto Maas, *Die Abstammungslehre*, pp 273–74

are faced with hard enamel so that the action of the upper teeth upon the lower keeps the cutting edges extremely sharp, these teeth do not form roots, but continue to grow throughout the lifetime of the animal Between the chisel like incisors and the grinding teeth, there is a long toothless gap, which, we assume, was in the ancestors of the rodents, occupied by the second and third incisors, the canine and two or more grinders This conclusion is justified by the facts of embryology, for instance in the embryo of the squirrel several of the missing teeth are begun as distinct tooth germs, but fail to develop, never cut the gum and are resorbed before birth

All available evidence points to the conclusion that birds are descended from reptiles a conclusion which is especially strengthened by the facts of palaeontology and will be examined more at length in the following lecture Such a descent explains many otherwise puzzling features in the ontogeny of birds, in which reptilian characteristics appear in transitory fashion and are either modified so as to take on typically bird like character, or are suppressed altogether A remarkable example of this is the formation of rudimentary teeth in certain embryonic birds, followed by their resorption and disappearance before hatching

It can hardly be contended that these rudimentary structures, which are confined to the embryonic stages of development and of which no trace remains in the adult, are so indispensable to the processes of ontogeny, that they were specially created to serve this temporary purpose For such a contention there is not a particle of evidence and the theory of evolution which regards these structures as useless remnants, due to inheritance from ancestors in which the structures are functional, offers much the most satisfactory solution of the problem that has yet been suggested

Embryology further shows that evolution is not invariably an advance from lower and simpler to higher and more complex types but may be by way of degeneration and degradation The adoption of a parasitic mode of life is very apt to cause such degradation, and some very remarkable instances of the degeneration of parasites have been observed An instructive example that may be cited is that of *Sacculina*, a nondescript creature that is parasitic on certain species of crabs The parasite is attached to the body of its victim, underneath the tail, by means of root like fibres which penetrate and ramify throughout the interior of the crab The root like fibres absorb nutriment and convey it to the body of the parasite, which is reduced to a

mere bag without appendages, muscles, nervous system sensory apparatus, digestive tract, or any determinable organs save those of reproduction The creature has the power of assimilating the nutritive juices which are conveyed to it by the root like filaments from the body of its host, and the power of reproduction and it must have some respiratory and excretory capacity, though there are neither gills nor glands From an examination of the adult parasite alone, it would be quite impossible to classify it and determine the type and class to which it should be referred, but embryology solves the problem From the egg is hatched a free swimming larva, which has jointed appendages, nervous, muscular and digestive systems and, in short, clearly belongs to that group of the Crustacea which includes the barnacles This is degeneration carried nearly to the utmost possible extreme and yet the individual development shows the derivation of this otherwise problematical parasite and the steps through which it passed in its deterioration

It was stated above that several distinguished naturalists altogether reject the recapitulation theory as a means of interpreting the facts of embryology They do this on the ground that inasmuch as changes and innovations in form or structure must arise in the germ plasm, at the very beginning of ontogeny, there is no reason why such changes might not involve the whole course of embryological development To my mind this a priori objection to the recapitulation theory is quite without force in view of the great body of observed facts, but there is no time to enter upon a discussion of such an abstract and difficult problem For our present purpose, however it is important to note that these objectors are staunch evolutionists and find in the community of mode in ontogeny between different classes of organisms one of the strongest arguments in support of the evolutionary doctrine.

CHAPTER X

EVIDENCES FROM PALAEONTOLOGY

STRENGTH AND WEAKNESS OF THE EVIDENCE

The word palaeontology means literally the science of ancient life. Practically, it is the study of the fossil remains of extinct animals and plants, including any traces of their existence, such as footprints, impressions in slate, clay, or coal The evidence from the fossils has definite elements of strength in that it deals with actual organisms that formerly inhabited the earth's surface Many of these species must have left descendants, some of which are doubtless living in a modified condition today Palaeontology should be able either strongly to support or to contradict the idea of evolution If its data accord with the evolution idea and are opposed to the special creation idea, the fossils may be said to be evidences of evolution

The weakness of the study of fossils lies in the fact that extremely few samples of the living forms that have existed in the past have been preserved, and of those that have been preserved only a very small percentage have been dug up and studied by capable scientists Many types of animals and plants, moreover, are soft and capable of preservation only under such exceptional conditions that but a rare specimen here and there over the world, scattered through various widely separated strata, has been found Only very common or abundant types are likely to have been preserved and discovered, for the chances of an uncommon form being preserved would be small and the further chances of these infrequently preserved specimens being found would be infinitely smaller

The great majority of fossil remains are fragmentary or preserved very incompletely, so that only the hard parts have come down to us There are, of course, many important exceptions to this rule, and these are our chief reliance in interpreting ancient life

That Darwin fully realized the vulnerable points in the palaeontological record is shown by the following quotation from the *Origin of Species*

"I look at the geological record as a history of the world imperfectly kept and written in a changing dialect, of this history we possess

the last volume alone, relating only to two or three countries Of this volume only here and there a short chapter has been preserved, and of each page only here and there a few lines Each word of the slowly changing language, more or less different in the successive chapters, may represent the forms of life which are entombed in our successive formations and which falsely appear to us to have been abruptly introduced"

OTHER OPINIONS AS TO THE ADEQUACY OF THE EVIDENCES FROM PALAEONTOLOGY

"The primary and direct evidence in favour of evolution can be furnished only by palaeontology The geological record so soon as it approaches completeness, must, when properly questioned, yield either an affirmative or a negative answer if Evolution has taken place there will its mark be left, if it has not taken place there will lie its refutation"—T H Huxley

"*The geological record is not so hopelessly incomplete as Darwin* believed it to be Since *The Origin of Species* was written our knowledge of that record has been enormously extended, and we now possess no complete volumes, it is true, but some remarkably full and illuminating chapters The main significance of the whole lies in the fact that, ***just in proportion to the completeness of the record is the unequivocal character of its testimony to the truth of the evolutionary theory***"—W B Scott

"On the other hand, matters have greatly improved since Darwin wrote his oft-cited Chapter X, many lands then geologically unknown have been explored and many of the missing chapters and paragraphs in the history of life have been brought to light The most ancient biologically intelligible period of the earth's history is called the Cambrian and, compared with the succeeding periods, the Cambrian has always been poor in fossils, great areas and thicknesses of rocks being entirely barren No one could doubt that our knowledge of Cambrian life was most incomplete and inadequate A few years ago Dr C D Walcott, Secretary of the Smithsonian Institution, discovered in the Canadian Rockies a most marvelous series of Cambrian fossils of an incredible delicacy and beauty of preservation, which have thrown a flood of new and unexpected light into very dark places It is clear that the Cambrian seas swarmed with a great variety and profusion of life, but that in only a few places, so far known to us

were conditions such that these delicate creatures could be preserved It is not possible to say how far the difficulty caused by the imperfection of the geological record will be removed by the progress of discovery Even as matters stand to-day, the astonishing fact is that so much has been preserved, rather than that the story is so incomplete Notwithstanding all the difficulties, the palaeontological method remains one of the most valuable means of testing the theory of evolution, because certain chapters in the history of life have been recorded with a minuteness that is really very surprising"—W B Scott *Theory of Evolution* (The Macmillan Company Reprinted by permission)

WHAT FOSSILS ARE AND HOW THEY HAVE BEEN PRESERVED

" Fossils are only animals and plants which have been dead rather longer than those which died yesterday "—T H Huxley

"Fossils are either actual remains of bones or other parts preserved intact in soil or rocks, or else and more commonly, parts of animals which have been turned into stone, or of which stony casts have been made All such remains buried by natural causes are called fossils "—Jordan and Kellogg

FOSSILS CLASSIFIED

Class 1 The actual remains of recently extinct animals and plants which have been buried or surrounded by some sort of preserving material constitute the first type under consideration Such remains have undergone little or no change of the original organic matter into inorganic. Thus we find the complete bodies of great hairy mammoths frozen in the arctic ice These are so well preserved that dogs have fed upon their flesh Nearly a thousand species of extinct insects including many ants, have been obtained practically intact from amber, a form of petrified resin Innumerable mollusk shells, teeth of sharks, pieces of buried logs, bones of animals buried in asphalt lakes and bogs have been found in a well preserved condition

Class 2 Petrified fossils —The process of petrification involves the replacement, particle for particle, of the organic matter of a dead animal or plant by mineral matter So completely is the finer structure preserved that microscopic sections of preserved tissues, especially of plants, have practically the same appearance as sections made from living organisms Various mineral materials have been employed in petrification, such as quartz, limestone or iron pyrites

Class 3 Casts and impressions —Very frequently the animal or plant has been buried in mud or has lain on a soft mud flat only long enough to have left its impress in the plastic material Subsequently the entire organism has decayed and been dissolved away, and its place has been taken by a mineral deposit Thus only the external appearance has been preserved, as would be the case in making plaster-of paris casts Sometimes traceries of soft bodied animals have been left upon forming slate or coal that are almost as accurate in detail as a lithograph

Perhaps the most remarkable fossils known are those found by *Professor Charles D Walcott in the marine oily shales of British* Columbia A large number of soft bodied invertebrates of Cambrian age have been found so wonderfully preserved that not only are the external features revealed, but sometimes even the details of the internal organs may be seen through the transparent integument

Some authorities include among fossils such traces of extinct life as footprints, utensils and tools of extinct man, and even the vestiges of archaic sea beaches Perhaps this is stretching the definition of the term ' fossil" too far

ON THE CONDITIONS NECESSARY FOR FOSSILIZATION

' Examination and study of the rocks of the earth reveal the fact that fossils or the remains of animals and plants are found in certain kinds of rocks only They are not found in lava, because lava comes from volcanoes and rifts in the earth's crust as a red hot viscous liquid, which cools to form a hard rock No animal or plant caught in a lava stream will leave any trace Furthermore, fossils are not found in granite, nor in ores of metals nor in certain other of the common rocks Many rocks are, like lava of igneous origin, others, like granite, although not originally in the melted condition have been so heated subsequent to their formation, that any traces of animal or plant remains in them have been obliterated Fossils are found almost exclusively in rocks which have been formed by the slow deposition in water of sand clay, mud, or lime The sediment which is carried into a lake or ocean by the streams opening into it sinks slowly to the bottom of the lake or ocean and forms there a layer which gradually hardens under pressure to become rock This is called sedimentary rock or stratified rock because it is composed of sedi

ment, and sediment always arranges itself in layers or strata In sedimentary or stratified rocks fossils are found The commonest rocks of this sort are limestone, sandstone, and shales Limestone is formed chiefly of carbonate of lime, sandstone is cemented sand, and shales, or slaty rocks, are formed chiefly of clay

"The formation of sedimentary rocks has been going on since land first rose from the level of the sea for water has always been wearing away rock and carrying it as sediment into rivers, and rivers have always been carrying the worn-off lime and sand and clay downward to lakes and oceans at the bottoms of which the particles have been piled up in layers and have formed new rock strata But geologists have shown that in the course of the earth's history there have been great changes in the position and extent of land and sea Sea bottoms have been folded or upheaved to form dry land, while regions once land have sunk and been covered by lakes and seas Again, through great foldings in the cooling crust of the earth which resulted in depression at one point and elevation at another, land has become ocean and ocean land And in the almost unimaginable period of time which has passed since the earth first shrank from its hypothetical condition of nebulous vapor to be a ball of land covered with water, such changes have occurred over and over again They have, however mostly taken place slowly and gradually The principal seat of great change is in the regions of mountain chains, which, in most cases are simply the remains of old folds or wrinkles in the crust of the earth

"When an aquatic animal dies, it sinks to the bottom of the lake or ocean, unless, of course, its flesh is eaten by some other animal Even then its hard parts will probably find their way to the bottom There the remains will soon be covered by the always dropping sediment. They are on the way to become fossils Some land animals also might, after death, get carried by a river to the lake or ocean, and find their way to the bottom, where they, too, will become fossils, or they may die on the banks of the lake or ocean and their bodies may get buried in the soft mud of the shores Or, again, they are often trodden in the mire about salt springs or submerged in quicksand It is obvious that aquatic animals are far more likely to be preserved as fossils than land animals. This inference is strikingly proved by fossil remains Of all the thousands and thousands of kinds of extinct insects, mostly land animals, comparatively few specimens are known as fossils On the other hand, the shell bearing

mollusks and crustaceans are represented in almost all rock deposits which contain any kind of fossil remains —Jordan and Kellogg[1]

The study of geology teaches us that the earth s outer zones have undergone within the period of vertebrate history numerous profound changes which in general we may term climatic changes There have been periods of continental subsidence, accompanied by ocean floor elevations, during which great continental plains have been covered with comparatively shallow seas The marine faunas of the seas have migrated into these shallows and representatives of them have been buried in sediment. When the reverse change has occurred and the continental plain has been again elevated the sedimentation of the shallow-sea period forms a great rocky stratum laden with marine fossils Between periods of subsidence millions of years elapsed, and therefore a break in the continuity of the entombed fossils is to be expected Discontinuity between the fossil faunas in adjacent strata is the invariable rule Were it not for this periodicity of subsidence and elevation there would be no boundaries between consecutive geologic strata

In addition to the methods of fossilization mentioned, a few others deserve notice Many animals of the arid plains have been fossilized by becoming imbedded in dust or sand drifts which have piled up against rocky outcrops or have filled in dried up arroyos Some very valuable fossils have been recovered from asphaltic deposits as the result of animals falling into liquid or semiliquid lakes or pools of asphalt

Not only are external organs preserved with precision but even delicate internal structures, such as the brains or the viscera of verte brates have been found in such a perfectly natural shape that the comparative anatomy could be worked out with confidence

On the whole, then, we must conclude that the earlier pessimism regarding the inadequacy and insufficiency of fossil data is giving way before a steadily increasing optimism due to the very rapid advance in technique and the surprisingly abundant discoveries of the modern palaeontologist The more enthusiastic of the new school of fossil hunters do not despair of ultimately bringing to light all of the really essential links in the chain of evidence necessary to place the evolution theory beyond the reach of controversy

[1] From D S Jordan and V L. Kellogg *Evolution and Animal Life* (copy right 1907) Used by special permission of the publishers D Appleton & Company

ON THE LAPSE OF TIME DURING WHICH EVOLUTION IS BELIEVED TO HAVE TAKEN PLACE

"*Independently of our not finding fossil remains of such infinitely* numerous connecting links [referring to the objection that all steps in the evolution of modern types should be revealed in the fossils], it *may be objected that time cannot have sufficed for so great an amount* of organic change, all changes having been effected slowly It is hardly possible for me to recall to the reader who is not a practical geologist, the facts leading the mind feebly to comprehend the lapse of time He who has read Sir Charles Lyell's grand work on the *Principles of Geology*, which the future historian will recognize as having produced a revolution in natural science, and yet does not admit how vast have been the past periods of time, may at once close this volume Not that it suffices to study the *Principles of Geology*, or to read special treatises by different observers on separate formations, and to mark how each author attempts to give an inadequate idea of the duration of each formation, or even of each stratum. We can best gain some idea of past time by knowing the agencies at work, and learning how deeply the surface of the land has been denuded, and how much sediment has been deposited As Lyell has well remarked the extent and thickness of our sedimentary formations are the result and the measure of the denudation which the earth's crust has elsewhere undergone Therefore a man should examine for himself the great piles of superimposed strata, and watch the rivulets bringing down the mud, and the waves wearing away the sea-cliffs, in order to comprehend something about the duration of past time, the monuments of which we see all around us "—Charles Darwin, *Origin of Species*

"In 1862," says Schuchert,[1] "the physicist, Lord Kelvin . . held that as our planet was continually losing energy in the form of heat, the globe was a molten mass somewhere between 20,000,000 and 400,000,000 years ago, with a probability of this state occurring about 98,000,000 years ago Finally in 1897 he concurred in Clarence King's conclusion that the globe was a molten mass about 24,000,000 years ago *Both of these conclusions*, however, were wrought out under the Laplacian hypothesis, and now many geologists hold that the earth never was molten While geologists have not been able to fit their evidence into so short a time, they have ever since been trying to keep their

[1] C. Schuchert, *Text-Book of Geology, Part II, Historical Geology* (1915)

MILLIONS OF YEARS						
	60 000 000 YEARS	AGE OF MAN	CENOZOIC		QUARTERNARY	ROCKS CHIEFLY UNMETAMORPHOSED SED MENTARY PREDOM NANT IGNEOUS SECONDARY ENTOMBED FOSS LS D RECT EV DENCE OF FORMER LIFE
60		AGE OF MAMMALS			TERTIARY	
	165,000 000 YEARS	AGE OF REPTILES	MESOZOIC		UPPER CRETACEOUS	
					LOWER CRETACEOUS COMANCHEAN	
					JURASS C	
225					TRIASSIC	
	450 000 000 YEARS	AGE OF AMPHIBIANS	PALAEOZOIC	LATE PALAEOZOIC	PERMIAN	
					PENNSYLVAN AN UPPER CARBONIFEROUS	
					M SS SSIPPIAN LOWER CARBON FEROUS	
		AGE OF FISHES		M D PALAEOZOIC	DEVONIAN	
					S LUR AN	
		AGE OF INVERTEBRATES		EARLY PALAEOZOIC	ORDOVICIAN	
675					CAMBRIAN	
	"PRECAMBRIAN" 825 000 000 YEARS	EVOLUT ON OF INVERTEBRATES	PROTEROZOIC	LATE PROTEROZOIC (ALGONKIAN)	KEWEENAWAN	ROCKS GENERALLY METAMORPHOSED IGNEOUS PREDOM NANT SED MENTARY SECONDARY LIMESTONE, IRON ORE AND GRAPH TE INDIRECT EV DENCE OF FORMER LIFE FOSSILS SCARCE
					ANIMIK AN	
					HURON AN	
				EARLY PROTEROZOIC	ALGOMIAN	
1 050					SUDBUR AN	
		EVOLUTION UNICELLULAR LIFE	ARCHAEOZOIC (ARCHEAN)		LAURENTIAN	
1 500					GRENV LLE KEEWAT N (COUTCH CH NG)	

FIG 30—Total geologic time scale, estimated at 1 500,000,000 years (*From Newman after Osborn*)

estimates within the bounds of Lord Kelvin s older calculations Walcott, in 1893, on the basis of the stratigraphic record and the known discharge of sediment by rivers concluded that 70,000 000 years had elapsed since sedimentation began in the Archeozoic Sir Archibald Giekie places the time at 100,000,000 years and most geologists have tried, although with difficulty, to fit the record within these estimates

' Since the discovery of radium all of the calculations previously made have been set aside by the new school of physicists, and now the geologists are told they can have 1 000 000 000 or more years as the time since the earth attained its present diameter Even if finally it shall turn out that the physicists have to reduce their estimates as to the age of certain minerals and rocks, geologists nevertheless appear to be on safer ground in accepting their estimates than those based either on sedimentation chemical denudation, or loss of heat by the earth "

The last decade has seen the demise of the outworn objection to evolution based on the idea that there has not been time enough for the great changes that are believed by evolutionists to have occurred. Given 100 000 000 or 1 000 000 000 years since life began, we can then allow 1,000 000 years for each important change to arise and establish itself We can also understand why it is that so little change can be noted in the majority of wild animals and plants within the historic period A thousand years in the development of the race is like a second in the development of an individual and though no one can notice any change in a growing creature in a second or a minute, very radical changes can be noted in an hour or a day or a year We cannot see any movement in an hour hand of a clock, but it moves with certainty around the dial in a relatively short time There is therefore no shortage of time Evolution may have been infinitely slow, but time has been infinitely long The accompanying time scale shows the lapse of time and the distribution in time of the main groups of animals (Fig 2)

ON THE PRINCIPAL GENERAL FACTS REVEALED BY A STUDY OF THE FOSSILS

1 None of the animals or plants of the past are identical with those of the present The nearest relationship is between a few species of the past and some living species which have been placed in the same genera.

2 The animals and plants of each geologic stratum are at least generically different from those of any other stratum, though belonging in some cases to the same families or orders

3 The animals and plants of the oldest (lowest) geologic strata represent all of the existing phyla, except the Chordata, but the representatives of the various phyla are relatively generalized as compared with the existing types

4 The animals and plants of the newest (highest) geologic strata are most like those of the present and help to link the present with the past

5 There is, in general, a gradual progression toward higher types as one proceeds from the lower to the higher strata

6 Many groups of animals and plants reached the climax of specialization at relatively early geologic periods and became extinct

7 Only the less specialized relatives of the most highly specialized types survived to become the progenitors of the modern representatives of their group

8 It is very common to find a new group arising near the end of some geologic period during which vast climatic changes were taking place Such an incipient group almost regularly becomes the dominant group of the next period, because it developed under the changed conditions which ushered in the new period and was therefore especially favored by the new environment

9 The evolution of the vertebrate classes is more satisfactorily shown than that of any other group, probably because they represent the latest phylum to evolve and most of their history coincides with the period within which fossils are known

10 Most of the invertebrate phyla had already undergone more than half of their evolution at the time when the earliest fossil remains were deposited

FOSSIL PEDIGREES OF SOME WELL KNOWN VERTEBRATES

PEDIGREE OF THE HORSE

Of all fossil pedigrees that of the horse is most often mentioned in evolutionary literature The main facts have been known for about forty years and there is a rather general consensus of opinion as to the history as a whole It appears practically certain that the horse family (Equidae) arose from a group of primitive five toed ungulates or hoofed mammals called Condylarthra that lived in Eocene times

No particular member of this extinct group has been found that fulfils all the requirements of a primitive horse ancestor, so the chances are that the real ancestral condylarthran has not been discovered

"The course of their [Equidae] evolution," says Dendy,[1] "has evidently been determined by the development of extensive, dry, grass-covered, open plains on the American continent In adaptation to life on such areas structural modification has proceeded chiefly in two directions The limbs have become greatly elongated and the foot uplifted from the ground, and thus adapted for rapid flight from pursuing enemies while the middle digit has become more and more important and the others, together with the ulna and the fibula, have gradually disappeared or become reduced to mere vestiges At the same time the grazing mechanism has been gradually perfected The neck and head have become elongated so that the animal is able to reach the ground without bending its legs, and the cheek teeth have acquired complex grinding surfaces and have greatly increased in length to compensate for the increased rate of wear As in so many other groups, the evolution of these special characters has been accompanied by gradual increase in size Thus *Eohippus*, of Lower Eocene times, appears to have been not more than eleven inches high at the shoulder while existing horses measure about sixty four inches, and the numerous intermediate genera for the most part show a regular progress in this respect

"All these changes have taken place gradually, and a beautiful series of intermediate forms indicating the different stages from *Eohippus* to the modern horse [*Equus*] have been discovered The sequence of these stages in geological time exactly fits in with the theory that each one has been derived from the one next below it by more perfect adaptation to the conditions of life Numerous genera have been described, but it is not necessary to mention more than a few"

The first indisputably horselike animal appears to have been *Hyracotherium*, of the Lower Eocene of Europe Another Lower Eocene form is *Eohippus*, which lived in North America, probably having migrated across from Asia by the Alaskan land connection which was in existence at that time In *Eohippus* the fore foot had four completely developed hoofed digits and a "thumb" reduced to a splint bone, in the hind foot the great toe had entirely disappeared and the little toe is represented by a vestigial structure or splint bone

[1] Arthur Dendy, *Outlines of Evolutionary Biology* (D Appleton & Company 1916)

Then came in succession *Orohippus*, of the Upper Eocene, *Mesohippus* of the Lower Miocene *Pliohippus* of the Upper Pliocene, and finally

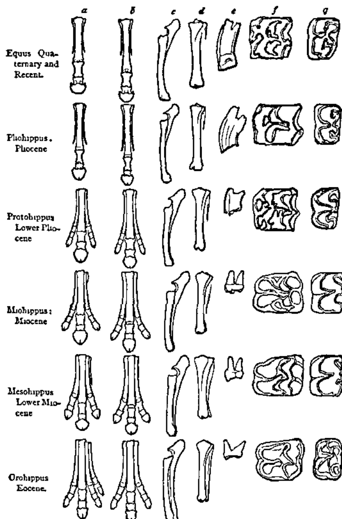


FIG 31.—Feet and teeth in fossil pedigree of the horse (*After Marsh*) *a*, Bones of the fore foot, *b*, bones of the hind foot, *c*, radius and ulna, *d*, fibula and tibia, *e*, roots of a tooth, *f* and *g* crowns of upper and lower teeth

Equus of the Quaternary and Recent Other genera might be mentioned, but the history of this series has been pictured in a classic

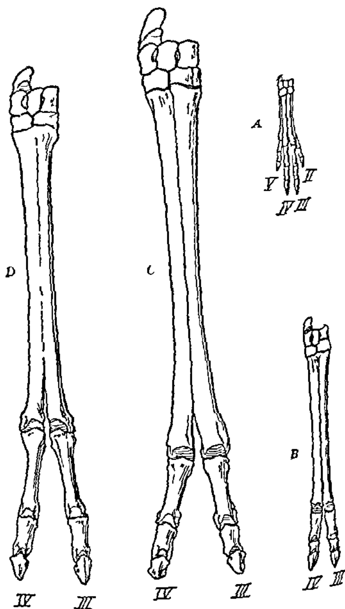


FIG 33 —Four stages in the evolution of the cameline fore foot *A Protylopus* Upper Eocene *B Poëbrotherium* Lower Oligocene *C Procamelus* Upper Miocene *D* guanaco Recent (*From Scott*)

Were there time enough to do so, we might trace the development of this family backward, step by step, through all the many stages between the Pleistocene and the Upper Eocene in quite as unbroken sequence and in as full detail as can be done for the horses We must, however, pass over all the intermediate steps and consider the ancestral camels of the Upper Eocene These were very little animals hardly larger than a jack rabbit, which had the full complement of teeth, 44 in total number, and all with very low crowns The limbs, and especially the feet, are relatively short, the ulna is complete and separate, as is also the fibula, there are four toes in each foot, though the lateral pair of the hind foot are extremely slender, and there is no co-ossification to form cannon bones The hoofs are well developed in form like those of an antelope, so that there can have been no pad For the present, the line cannot be carried back of the Upper Eocene the probable ancestors from the middle and Lower Eocene being, as yet, represented only by fragmentary specimens

In addition to this main stem of cameline descent which resulted in the modern species, there were two short lived side branches which should be mentioned One, ending in the Lower Miocene, was the series descriptively called "gazelle-camels," small animals with very long and slender legs, evidently swift runners The other series, the so-called "giraffe-camels," terminated in the Upper Miocene, these were browsers and display an increasing stature, especially in the length of the neck and fore limbs They adapted themselves to the growing aridity of the western plains

EVOLUTION OF THE ELEPHANTS[1]

A FRANKLIN SHULL

The mastodon elephant series shows a larger number of obvious changes than most of the other series named, all of these changes except that of the body having to do with features of the head From the numerous specimens of elephant like forms available, the following are selected (following Lull) as probably representing a direct line of evolution *Moeritherium* from the Upper Eocene of Egypt, *Palaeomastodon* from the Lower Oligocene of Egypt, also from India, *Trilophodon* from the Miocene of Europe, Africa and North America, *Mastodon* from the Pliocene and Pleistocene of

[1] From A F Shull *Principles of Animal Biology* (copyright 1920) Used by special permission of the publishers The McGraw Hill Book Company

North America, Europe and Asia, *Stegodon* from the Pliocene of southern Asia, and *Elephas* from the Pleistocene of the Americas, Europe, and Asia, as well as the living elephants of Asia and Africa.

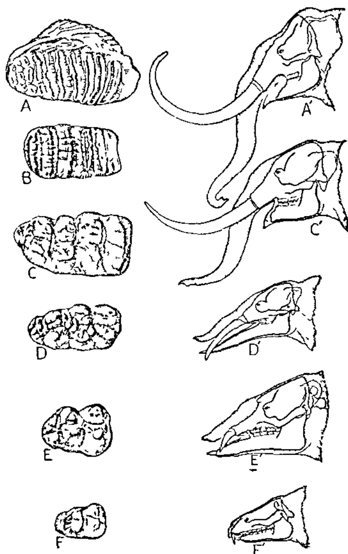


FIG. 4.—Evolution of head and molar teeth of mastodons and elephants. *A*, *A′*, *Elephas*, Pleistocene, *B*, *Stegodon*, Pliocene, *C*, *C′*, *Mastodon*, Pleistocene; *D*, *D′*, *Trilophodon*, Miocene, *E*, *E′*, *Palaeomastodon*, Oligocene, *F*, *F′*, *Moeritherium*, Eocene (From Lull)

A study of Figure 34 in connection with the following account will disclose the more striking steps of evolution These forms differed from one another in a number of features, but the differences between any member of the series and the one that precedes or that which follows were so small that the series is obviously a continuous one *Moeritherium* was very different from the modern elephant, but the intermediate forms completely bridged the gap The series exhibits an enormous increase in size of body changes in the form and size of the teeth, a reduction in the number of teeth, an alteration in the method of tooth succession the enlargement of certain teeth to become tusks, the elongation and subsequent shortening of the lower jaw, the development of the upper lip and nose into a proboscis, and an increase in the height of the skull through the development of large cavities in the substance of the bone These features are described in the several forms seriatim

Moeritherium.—The earliest animal recognized as belonging to the elephant series, *Moeritherium* by name, was recovered from the late Eocene and early Oligocene deposits of northern Egypt It was slightly over three feet in height The features suggesting elephantine affinities are the high posterior portion of the skull (Fig 34, *F*), composed of somewhat cancellate bone that is, bone containing open spaces, the elongation of the second pair of incisors in each jaw to form short tusks the indication of transverse ridges on the molar teeth (Fig 34 *F*), and the position of the nasal openings some distance back of the tip of the upper jaw indicating probably a prehensile upper lip There were 24 teeth, and the neck was long enough to enable the animal to put its head to the ground It probably fed upon tender shoots and swamp vegetation

Palaeomastodon —This form also lived in Egypt, but has recently been found in India It dates from early Oligocene time *Palaeomastodon* was of somewhat larger size than the preceding form, the posterior part of the skull was distinctly higher (Fig 34, *E'*)—with a greater development of cancellate bone, and the neck was somewhat shortened The upper incisors of the second pair were more elongated as tusks and bore a band of enamel on their front surfaces The lower second incisors were present, but not enlarged All other incisors and the canines had disappeared The molar teeth (*E*) resembled those of *Moeritherium* but were larger The lower jaw was considerably elongated, and the total number of teeth was still high (26) The nasal openings had receded until they were just in front of the eyes,

which is believed to indicate the existence of a short proboscis extending at least to the tips of the tusks

Trilophodon.—*Trilophodon*, a great migrant and consequently wide spread over several continents as stated above, exhibited in several respects a striking advance over *Palaeomastodon*, but this advance was in the main in the same direction as was indicated by the change from *Moeritherium* to *Palaeomastodon* *Trilophodon* was a huge animal, nearly as large as modern Indian elephants The tusks were considerably longer (Fig 34, *D'*) and still bore a band of enamel The molar teeth were large and greatly reduced in number, so that only two were present at any one time on each side of each jaw The surface of these teeth bore a somewhat larger number of transverse crests (Fig 34 *D*) than were present in the earlier forms The lower jaw was enormously elongated, so that it projected as far forward as the tusks The great weight of the lower jaw and tusks was associated with a considerable development of cancellate bone in the skull, to which the supporting muscles of the neck were attached Presumably there was a proboscis which extended to or beyond the tips of the tusks and lower jaw

Mastodon —The mastodons on the whole represent a line of development which became extinct, but in their incipient stages they appear to have given rise to the succeeding forms leading to the elephants The body was somewhat larger than that of *Trilophodon* being about the size of the Indian elephant The tusks (*C'*) were much elongated (9 feet or more), but the lower jaw was greatly shortened and the lower incisor teeth were reduced or wanting The molar teeth (Fig 34, *C*) were scarcely more complex than earlier forms, and numbered two on each side of each jaw They were still crushing teeth, and the food must have been tender twigs and succulent plants, indeed, remains of such objects have been found in the region of the stomach of the fossil mastodons

Stegodon —This animal is of interest chiefly because the molar teeth bore five or six well defined transverse ridges (Fig 34, *B*) These ridges were due to plates of *enamel* extending up through the tooth, and inclosing a substance known as *dentine* Over the enamel in an unworn tooth was a thin coat of a third substance called *cement*, but there was not much of this substance between the ridges In the latter respect *Stegodon* differed, as is pointed out below, from the elephants and mammoths On the whole, *Stegodon* was intermediate between the mastodons and elephants

Elephas—In this genus are included a number of extinct forms (the mammoths) from three or four continents, and the living elephants The extinct forms, though called mammoths, were not large animals, being no larger than the Indian elephant of today, and not so large as the living African species Some of the features of the elephants, their size, the short neck, the long proboscis and the heavy tusks are matters of common observation The skull is very high and short (Fig 34 A') The height is due chiefly to the development of cancellate bone, not to the enlargement of the brain, which is still quite small. As stated above, the high skull affords the necessary leverage for the muscles that support the weight of the tusks The molar teeth are distinctly grinding teeth (Fig 34, A) Each tooth bears a number of transverse ridges, about ten in the African elephant and two dozen or more in the Indian species These ridges are worn down by the chewing of harsh food, so that the upper surface displays a number of flattened tubular plates of enamel inclosing dentine and bound together by cement A tooth is completely worn out by use and is replaced by another The method of replacement, however is peculiar While the tusks (incisors) are of two sets, one following the other like milk and permanent teeth of other mammals, the grinders succeed one another in continuous fashion There are never more than two visible grinders on each side of each jaw As they wear out they move forward in the jaw, and are replaced by new teeth appearing behind New molars thus enter at intervals of two to four years in young elephants, and at intervals of 15 to 30 years in later life If an elephant lives long enough (60 years or more) it develops a total of 28 teeth including tusks, but has not more than ten (often less) at any one time

Correlated with the nature of the teeth of the elephants are their food and chewing habits Whereas the ancestral forms whose molars bore prominent elevations lived on twigs and tender herbage which they crushed in mastication the mammoths with their flattened tooth surfaces devoured grasses, sedges and other harsh vegetation which they ground with lateral motion of the teeth upon one another In this respect modern elephants are like the mammoths

In the changes described above is found one of the most beautiful and best established evolutionary series with which the palaeontologist is acquainted Only a few others equal or approach it in clearness and completeness

CHAPTER XI

THE EVOLUTION OF MAN PALAEONTOLOGY[1]

RICHARD SWANN LULL

ORIGIN OF PRIMATES

Stock —There is but little doubt that two important orders of modern mammals the Carnivora and the Primates, had a common origin diverging mainly along lines determined by a dietary contrast, as the former have become more strictly flesh eating or predaceous, the latter largely fruit eating and as a consequence more completely arboreal Back of each group lie as annectant forms the Insectivora, not perhaps such as are alive to day, as all these are highly specialized along diverse lines, but generalized insectivores possessing, because of their primitiveness a wider range of potential adaptation Matthew is disposed to think of these, our distant ancestors, at the dawn of the Tertiary, as a sort of hybrid between a lemur and a mongoose, rather catholic in their tastes living among and partly in the trees with sharp nose bright eyes and a shrewd little brain behind them looking out if you will from a perch among the branches, upon a world that was to be singularly kind to them and their descendants ' Thus we can define the stock as a relatively large brained arboreal insectivore, of primitive but adaptable dentition, and especially of progressive mentality

Time —The time of primate origin must have been not later than basal Eocene, as primates, clearly definable as such, are found in the Lower Eocene rocks of both Europe and North America

Place —The simultaneous appearance of the primate in the Old World and the New gives rise to the same conclusions as to their place of origin and their migrations thence as with other modernized mammals It suffices now to say that their ancestral home was boreal Holarctica, probably within the limits of the present continent of Asia, whence they migrated southward along the three great continental radii The impelling cause of this migration was the increasing northern cold, before which the boreal limitations of the *tropical forests retreated, carrying with them the primates which,* in

[1] From R. S Lull *Organic Evolution* (copyright 1917) Used by special permission of the publishers The Macmillan Company

general, are utterly dependent upon such an environment for their sustenance

Geologic record.—Primates are found in the North American sediments from Lower to Upper Eocene time, when they became extinct Thus, while their remains constitute a relatively large percentage of the total fauna of the Eocene, primates are utterly unknown on this continent from that time until the coming of man In Europe the record is similar except that the extinction occurred at a somewhat later date, the Oligocene Furthermore, they reappear in Europe in the Lower Miocene at the time of the proboscidean migration out of Africa whence these primates may also have come Their second European extinction was in the Upper Pliocene shortly before the first appearance of mankind

But in southern Asia, Africa, and South America the evolution of primates seems to have been continuous since the first great southward migration The evidence, however, is not so much the historical documents as the presence of primates in those places at the present time, the fossil record is not entirely lacking although highly incomplete The South American monkeys may have had their origin in the ancient North American primates, or more doubtfully, the stock may have come by way of Africa Scott inclines toward the latter view although he says the evidence is by no means conclusive

ORIGIN OF MAN

Stock—According to W K Gregory, the stock from which man arose was some big brained anthropoid related most nearly to the chimpanzee-gorilla group, an assumption based upon anatomical evidences, in spite of wide differences in habitus and consequent adaptation

Place—Evidences point to central Asia as the place of descent from the trees of the human precursor the reasons for this belief being several First, it was central for migrations elsewhere, Europe, on the other hand, where the most conclusive, in fact almost the exclusive evidence for fossil man is found, is too small an area for the divergent evolution of the several human species Second Asia is contiguous to the oldest known human remains, which as we shall see were found in Java Third, it was the seat of the oldest civilizations, not only of *the existing nations which, like the Chinese trace their recorded* history back to a hoary antiquity, but of nations which preceded them by thousands of years and whose records have not yet come to light

This antiquity vastly exceeds that of the nations of Europe or of the Americans or of Africa Fourth, central Asia is the source of almost all of our domestic animals, many of which have been subjected to human will and control for thousands of years and this is equally true of many of our domestic plants This is not due to the fact that man first reached civilization in Asia but rather that he chose for his companions the highest and best of their several evolutionary lines, and Asia was the place of all others upon earth where the evolution in general of organic life reached its highest development in late Cenozoic time (Williston) Fifth climatic conditions in Asia in the Miocene or early Pliocene were such as to compel the descent of the prehuman ancestor from the trees a step which was absolutely essential to further human development

Impelling cause —We look for a geologic cause back of this most *momentous crisis in the evolution of humanity* and we find *it in conti*nental elevation and consequent increasing aridity of climate, especially to the northward of the Himalayas With this increased aridity and tempering of tropical heat came the dwindling of the forested areas suitable to primate occupancy Barrell has suggested that this diminution left residual forests comparable to the diminishing lakes and ponds of the Devonian which upon final desiccation compelled their denizens to become terrestrial or perish The dwindling of the residual forests would have an effect upon the tree-dwellers which may be expressed in precisely the same words. Once upon the ground the effect upon even a conservative type—and the primates in general where constant conditions prevail, are slow of change—would be the rapid acquisition of such adaptations as were necessary to insure survival under the new conditions The other man like apes had, unfortunately for their further evolution, reached a region where tropical forests continued to be available and hence have retained their arboreal life and with it a stagnation of progress The result has been at any rate on the part of the three larger forms, a degeneracy from the estate of their common ancestry with mankind, the gibbons seem to have deteriorated less, while terrestrial man has risen to the summit of primate evolution

Time —The time of the descent is not later than early Pliocene nor earlier than Miocene time, when the terrestrial ape man became what we would call human was perhaps later, but certainly during the Pliocene, which makes the age of man as such measurable in terms of hundreds of thousands of years!

Significance of the descent from trees—As a result of the descent from the trees, certain definite factors were called into play, each of which had its effect on the further evolution Briefly enumerated, these are (1) Assumption of the erect posture, (2) liberation of the hands from their ancient locomotor function to become organs of the mind, (3) loss of the easily obtainable food of the tropical forests necessitating the search for sustenance, both plant and animal, and man became a hunter, (4) need of clothing with increasing inclemency of the weather, especially during the long winters, (5) freedom from climatic restrictions—when an omnivorous diet and clothing were acquired man was no longer limited to one definite habitat and the result was dispersal, (6) the development of communal life, rendered possible by the terrestrial habitat Primates are at best gregarious, submitting, as in the gorilla, to the leadership of the strongest male, but it is only by communal life with its attendant division of labor that man can rise above the level of utter savagery

Evolutionary changes—Human evolutionary changes which are recorded are more erect posture, shorter arms, perfection of thumb opposability, reduction of muzzle and of size of teeth, loss of jaw power, development of chin prominence, increase in skull capacity, diminution of brow ridges, diminution in strength of zygo matic or temporal arch, increase in size and complexity of brain especially frontal lobes, development of articulate speech

FOSSIL MAN

Fossil remains of man are found under two conditions, in river valley deposits and in limestone caverns which served first as a dwelling place and later as a sepulture Of these the caverns have been by far the most productive, but they contain only the remains of the later races, as the caverns according to Penck did not become available for human occupancy before middle Pleistocene time.

The rarity of human fossils may be explained, first, by the various burial customs which seldom are sufficiently perfect to preclude the possibility of alternate wetting and drying or of rapid oxidation both of which are prohibitive of fossilization If man lived and died in the forests the chances for his fossilization, in common with other forest creatures, was very remote, for the remains of such are almost invari ably destroyed by other animals, by dampness, or by fungi, and rarely attain a natural burial in sediment If on the other hand he dwelt

in the open, the chances of so shrewd a creature being caught in the flood waters and thus buried in sediment were not very great However we account for it, the fact remains that relics of ancient man are rare and are valued accordingly

In North America —Repeated instances of seemingly ancient man have been brought to light in North America, such as the "Calaveras skull" of the California gold bearing gravels, which was satirized by Bret Harte, the Nebraska "Loess man," and those of the Trenton gravels, none of which, with the possible exception of the last-mentioned, has proved to be really old in the geologic sense Indirect evidence of human antiquity, that is, the association of North American man with animals which are now extinct, while very rare, has been reported in at least two highly authentic instances The first of these was at Attica, New York, and is attested by Doctor John M Clarke, the New York state geologist Four feet below the surface of the ground, in a black muck, he found the bones of the mastodon (*Mastodon americanus*), and 12 inches below this, in undisturbed clay, pieces of pottery and thirty fragments of charcoal The charcoal may have been of natural origin, but the presence of the pottery seems conclusive The other instance was that of the remains of a herd of extinct bison (*Bison antiquus*) found near Smoky Hill River, Logan County, Kansas, and thus described by Professor Williston An "arrow head was found underneath the right scapula of the largest skeleton, embedded in the matrix, but touching the bone itself The skeleton was lying upon the right side The bone bed when cleared off contained the skeletons of five or six adult animals, and two or three younger ones, together with a foetal skeleton within the pelvis of one of the adult skeletons The animals had evidently all perished together, during the winter There was no possibility of the accidental intrusion of the arrow head in the place where found . It must have been within the body of the animal at the time of death, or have been lying on the surface beneath its body "

What at this writing is claimed to be another genuine case of such an association, this time of the actual human bones, has just been announced from Florida This find, which has been reported by State Geologist Sellards, was made at Vero, eastern Florida, in 1913 The fossil human bones are from two incomplete skeletons and are found in strata which also contain remains of the following extinct species *Elephas columbi*, *Equus leidyi*, a fox, a deer, the ground sloth, *Megalonyx jeffersoni*, and the American mastodon

In South America —A number of finds have been recorded from South America notably by the late Florentino Ameghino of Buenos Aires who contributed so largely to our knowledge of South American prehistoric life An expert from Washington, Doctor Ales Hrdlicka, has studied with the utmost care the locality and character of each of these finds in the Western World, and has expressed the opinion that none is of an antiquity greater than that of the pre-Columbian Indians

Further evidence lies in the uniformity of type, except for minor distinctions of all native American peoples There is no such racial differentiation as that seen in the Old World, and the argument is that there has not been time for such a deployment The area and conditions as an adaptive radiation center are surely ample

In Africa —The only African relics thus far reported are those of prehistoric cultures, comparable to those of Southern Europe, in certain caverns of the Barbary States There has also been reported from Oldoway ravine, German East Africa, a human skeleton of undoubted antiquity It is described, however, as being neither a very early nor a primitive type

In Asia —Asia has given us in *Pithecanthropus* the oldest known relic of the Hominidae found at Trinil in the island of Java Osborn says "It is possible that within the next decade one or more of the Tertiary ancestors of man may be discovered in northern India among the foothills known as the Siwaliks Such discoveries have been heralded, but none have thus far been actually made Yet Asia will probably prove to be the center of the human race We have now discovered in southern Asia primitive representatives or relatives of the four existing types of anthropoid apes namely, the gibbon, the orang the chimpanzee, and the gorilla, and since the extinct Indian apes are related to those of Africa and of Europe, it appears probable that southern Asia is near the center of the evolution of the higher primates and that we may look there for the ancestors not only of prehuman stages like the Trinil race but of the higher and truly human types '

In Europe —It is in Europe, however, that the tale of human prehistory is the most complete, not only through the happy accident of preserval but because it has been much more thoroughly explored than has the Asiatic evolutionary center The latter, however, holds the greatest hopes for future exploration since, as we have emphasized Europe is too small to be an adaptive radiation center and European

prehistoric man represents waves of migration from the greater continent

Nevertheless the European record has enabled us to name and define a number of distinct human species, and here the record of the cultural evolution of man is also unusually complete Hence European chronology is taken as a standard in describing discoveries from any portion of the world

CHRONOLOGICAL TABLE

(Adapted from Osborn 1915)

POSTGLACIAL TIME	25 000 years
Upper Palaeolithic culture	
Crô-Magnon man	
FOURTH GLACIAL STAGE (Wurm Wisconsin)	50 000 years
Close of Lower Palaeolithic culture	
Neanderthal man	
[illegible]	150 000 years
[illegible]	175 000 years
SECOND INTERGLACIAL STAGE	375 000 years
Heidelberg man	
SECOND GLACIAL STAGE (Mindel Kansas)	400 000 years
FIRST INTERGLACIAL STAGE	475 000 years
Pithecanthropus ape man	
FIRST GLACIAL STAGE (Gunz Nebraskan)	500 000 years

Pithecanthropus —The Java ape man *Pithecanthropus erectus* (Fig 35) was discovered in Trinil, on the Solo or Bengawan River in central Java, in 1894 The type consists of a calvarium or skull cap, a left thigh bone, and two upper molar teeth The skull is characterized by its limited capacity about two-thirds that of man and by the low flat forehead and beetling brows Hence not only was the brain limited in its total size, but this was especially true of the frontal lobes, which, as we have seen, are the seat of the higher intellectual faculties Thus, as Osborn says, although touch, taste, and

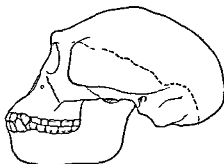


FIG 35 —Skull of Java ape man *Pithecanthrop s erectus* (From Lull, after Dubois)

vision were well developed there was a limited faculty for profiting by experience and accumulated tradition The femur associated with the skull is remarkable for its length and slight curvature as compared with the primitive Neanderthal race of Europe and indicates a creature fully as erect and nearly as tall as the average European of today the height being estimated at 5 feet 7 inches as compared with 5 feet 3 inches for the Neanderthals and 5 feet 8 inches the average height of modern males The erect posture of course implies the liberation of the hands from any part in the locomotor function The teeth are somewhat ape-like but are more human than are those of the gibbon and the human mode of mastication has been acquired Certain authorities have tried to prove that *Pithecanthropus* is nothing but a large gibbon, but the weight of authority considers it prehuman though not in the line of direct development into humanity It is nevertheless a highly important transitional form

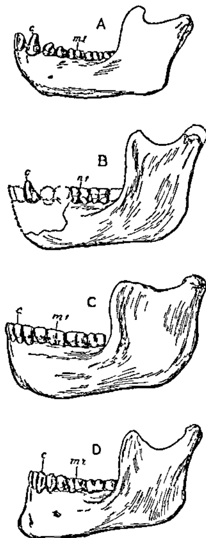


FIG 36 —Jaws left outer aspect of *A* chimpanzee *Pan* sp *B* fossil chimpanzee *Pan vetus* found in association with Piltdown man *C* Heidelberg man *Homo heidelbergensis* *D* modern man *H sapiens* (*From Lull after Woodward*)

Associated with the *Pithecanthropus* remains are those of a number of the contemporary animals which fix the date as either of the Upper Pliocene or lowermost Pleistocene period which being rendered in terms of years gives an estimated age of about 500 000!

Heidelberg man.—*Homo heidelbergensis*, the Heidelberg man represents the oldest recorded European race, geologically speaking The type was discovered in 1907 in river sands, 79 feet below the surface, at Mauer, near Heidelberg, South Germany The relic consists of a perfect lower jaw with the dentition (Fig 36, *C*) The description by the discoverer, Doctor Schoetensack, follows (from Osborn)

'The mandible shows a combination of features never before found in any fossil or recent man The protrusion of the lower jaw just below the front teeth (the chin prominence) which gives shape to the human chin is entirely lacking Had the teeth been absent it would have been impossible to diagnose it as human From a fragment of the symphysis of the jaw it might well have been classed as some gorilla like anthropoid while the ascending ramus resembles that of some large variety of gibbon The absolute certainty that these remains are human is based on the form of the teeth—molars, premolars canines and incisors are all essentially human and although somewhat primitive in form show no trace of being intermediate between man and the anthropoid apes but rather of being derived from some older common ancestor The teeth, however, are small for the jaw, the size of the border would allow for the development of much larger teeth We can only conclude that no great strain was put on the teeth and therefore the powerful development of the bones of the jaw was not designed for their benefit The conclusion is that the jaw, regarded as unquestionably human from the nature of the teeth, ranks not far from the point of separation between man and the anthropoid apes In comparison with the jaws of the Neanderthal races we may consider the Heidelberg jaw as pre-Neanderthaloid, it is in fact, a generalized type '

Associated with the Heidelberg jaw is an extensive warm-climate fauna straight tusked elephant (*E antiquus*), Etruscan rhinoceros primitive horse, bison wild cattle (*urus*), bear lion, and so on, all of which aid in establishing the date of the jaw as Second Interglacial and its age, conservatively estimated, at from 300 000 to 375,000 years The cultural evolution of Heidelberg man is indicated by the presence of eoliths, flint implements of the crudest workmanship, if indeed their *apparent fashioning is not merely the result of use*

Neanderthal man.—The original specimen of the Neanderthal man, *Homo neanderthalensis* or *primigenius* (Figs 37, 38, 39) was discovered in 1856 not far from Düsseldorf in Rhenish Prussia Here the valley of the Düssel forms the deep Neanderthal ravine, whose

limestone walls are penetrated by caverns in one of which the remains were found What was doubtless a perfect skeleton at the time of its

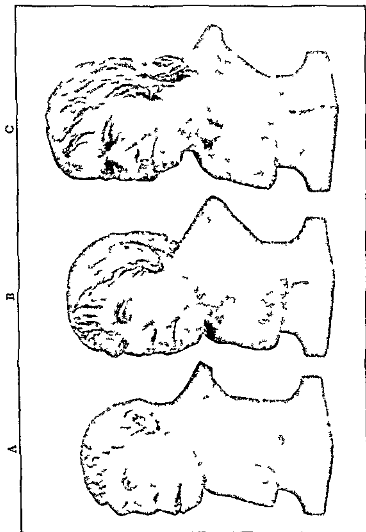


FIG 37 —Restoration of prehistoric men after models by J H McGregor *A Pithecanthropus erectus* the ape-man of Java *B Homo neanderthalensis* the Neanderthal man of Europe *C Homo sapiens* the Cro-Magnon man of Europe (*From Lull by courtesy of Professor McGregor*)

discovery was so injured by its finders that only a portion of it which is now preserved in the Provincial Museum at Bonn was saved This prophet of an unknown race was for a time utterly without honor

though of course the subject of a most heated controversy, being considered as non human, or, as Virchow believed, owing its distinctive characters to disease The sagacity of Huxley threw true light upon the problem, though it was not until the mute testimony of other representatives of the race (the men of Spy) was offered that even Huxley's masterful conception of the Neanderthal characters was taken as an accepted fact

Professor Huxley's description of the Neanderthal type is classic He says

"The anatomical characters of the skeletons bear out conclusions which are not flattering to the appearance of the owners. They were short of stature but powerfully built, with strong, curiously curved thigh bones the lower ends of which are so fashioned that they must have walked with a bend at the knees

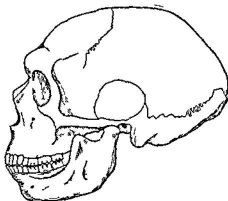


FIG 38 —Neanderthaloid skull of La Chapelle aux Saints (*Homo neanderthalensis*) (*From Lull after Boule*)

Their long depressed skulls had very strong brow-ridges, their lower jaws, of brutal depth and solidity, sloped away from the teeth downwards and backwards in consequence of the absence of that especially characteristic feature of the higher type of man, the chin prominence"

Subsequently several more specimens have come to light, at Spy in Belgium, at Krapina in Croatia, at Le Moustier, La Chapelle-aux Saints and La Ferrassie in France, and at Gibraltar, which, while differing in various details, effectually serve to establish the race, whose main characteristics are Heavy, overhanging brows, retreating forehead, long upper lip, jaw less powerful than that of the Heidelberg man but very thick and massive, chin generally strongly receding but in process of forming, dentition extraordinarily massive in the La Chapelle specimen, whereas in those of Spy the teeth are small The skull in many characteristics is nearer to the anthropoids than to modern man

The brain is large and its volume is surely human, but the proportions are again less like those of recent man than like the anthropoids. The chest is large and robust, the shoulders broad, and

the hand large, but the fingers are relatively short, the thumb lacking the range of movement seen in modern man The knee was somewhat bent, the leg powerful, with a short shin and clumsy foot, clearly not of cursorial adaptation The curve of the bent leg was correlated with a similar curvature of the spine, so that the man could not stand fully erect, as he lacked the fourth or cervical curvature of *Homo sapiens* The average stature was 5 feet 3 inches, with a range from 4 feet 10 3 inches to 5 feet 5 2 inches, partly sex differences

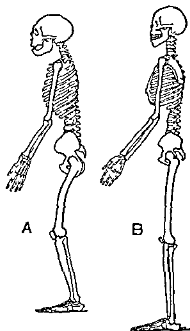


FIG 39 —Skeleton of Neanderthal man *A Homo neanderthalensis* compared with that of a living native Australian *B Homo sapiens* the latter the lowest existing race (*From Lull after Woodward*)

Neanderthal man lived in Europe from the Third Interglacial stage through the Fourth Glacial, a duration of thousands of years, and then became extinct, from twenty to twenty five millenniums ago He seems to have been an actual lineal successor of the man of Heidelberg but was throughout his long career an unprogressive static race One of the most remarkable features in connection with this race, however, was the very reverent way in which the dead were buried with an abundance of ornaments and finely worked flints This can have but one interpretation, the awakening within this ancient type of the instinctive belief in immortality!

Piltdown man —In 1912 was announced the discovery of a very ancient man from the Thames gravels at Piltdown, Sussex, England Here again the skull was injured and partly lost, so that the question of its proper restoration has been the subject of considerable controversy The material consists of portions of the cranial walls, nasal bones, a canine tooth, and part of a lower jaw The brain case in this instance is typically human, except for the remarkably thick cranial walls The forehead is high and lacks the superorbital ridges of Neanderthal man and *Pithecanthropus* While the skull is of com-

paratively high human type, the associated jaw and canine tooth clearly are not, and some difficulty was met in explaining their evolutionary discrepancy That has apparently been answered, however, by the conclusion that the association of the material is purely accidental and that the jaw not only does not belong with the skull, but that it is not even human but is that of a fossil chimpanzee That being the case, there seems to be no reason for the exclusion of the Piltdown man, who has been named *Eoanthropus dawsoni*, from the direct line of human ancestry The specimen is not, perhaps, so surely dated as are those of the other European races, but it is associated with a warm-climate fauna and is generally considered to belong to the Third Interglacial stage—from 100,000 to 150,000 years old, and hence vastly more ancient than the more primitive *Homo neanderthalensis* (See Fig 36, *B*)

Crô-Magnon man —The original finds of the men of the Crô Magnon race *Homo sapiens*, were made at Gower, Wales, and at Aurignac France In the latter place seventeen skeletons came to light in 1852, but were buried in the village cemetery and thus lost to science, and not until 1868, when five more skeletons were discovered at Crô-Magnon, France, was the race established These individuals, an old man, two young men, a woman and a child, are thus the types of the race This magnificent race is thus characterized

Skull large but narrow, with a broad face, hence disharmonic. Facial angle equalling the highest type of *Homo sapiens* Jaw thick and strong, with a narrow but very prominent chin Forehead high and orbital ridges reduced Brain not only of high type but very large, that of the women exceeding the average male of to-day

The stature of the old man was 6 feet 4 5 inches, the average for males being 6 feet 1 5 inches, for women 5 feet 5 inches, a great disparity The lower segments of the limbs were long, in contrast with the Neanderthal type, hence the men of Crô-Magnon were swift footed, while those of Neanderthal were slow Osborn says "The wide, short face, the extremely prominent cheekbones, the spread of the palate and a tendency of the upper cutting teeth and incisors to project forward, and the narrow, pointed chin recall a facial type which is best seen to-day in tribes living in Asia to the north and to the south of the Himalayas As regards their stature the Crô-Magnon race recall the Sikhs living to the south of the Himalayas In the disharmonic proportions of the face, that is, the combination of broad cheekbones and narrow skull, they resemble the Eskimo The

sum of the Crô-Magnon characters is certainly Asiatic rather than African, whereas in the Grimaldis (of which specimens have been found in association with Crô-Magnons at the Grotte des Enfants, Mentone) the sum of the characters is decidedly negroid or African "

The Crô-Magnons again show by their elaborate burial customs how old and well founded is the belief in life after death They are supposed to be the people who left on the walls of the caverns of France and Spain the marvelous examples of Upper Palaeolithic art of which Professor Osborn's book gives so adequate a description They lived for a while contemporaneously with the men of Neanderthal and may have contributed somewhat to the final extinction of the latter In the course of time, however, they too declined, although to this day survivors of the race may be seen in Dordogne, at Landes near the Garonne in Southern France, and at Lannion in Brittany Osborn says

The decline of the Crô Magnons, with their artistic culture, "may have been partly due to environmental causes and the abandon ment of their vigorous nomadic mode of life, or it may be that they had reached the end of a long cycle of psychic development We know as a parallel that in the history of many civilized races a period of great artistic and industrial development may be followed by a period of stagnation and decline without any apparent environmental cause'

Europe was repopulated after Crô-Magnon decline by later invaders from the Asiatic realm, the so-called Mediterranean narrow headed and the Alpine broad headed types, etc, probably differen tiated in Asia in early Palaeolithic times The repopulation took place in the Upper Palaeolithic

EVIDENCES OF HUMAN ANTIQUITY

Great variation.—These, briefly summarized, are, first, great variation If man is monophyletic, that is derived from a single prehuman species, and there is no reason to believe otherwise he must be old, for while the adaptations to ground-dwelling after the descent from the trees were doubtless relatively rapidly acquired the differen tiation into the various races due perhaps largely to climatic influ ences rather than to any notable environmental change, must have been slowly attained As corroborative evidence we have but to point to the mural paintings on Egyptian monuments, dating back

several thousand years, in which are depicted the Ethiopian Caucasian and the like, which are in some instances striking likenesses of the present day Egyptians

Universal distribution is, in animals another mark of antiquity in man, it is probably less so because of his greater intelligence And yet before transportation had become a science man's spread over land and sea was extremely slow

High intelligence as compared with that of the anthropoids is also a mark of antiquity for the brain especially the type of brain found in the higher human races must have been very slow of development Our study of fossil man shows this

Communal life, division of labor and all of the complicated interactions which it brings about, and the development of law and religions all have taken time When we realize that Babylonian texts twice as remote as the patriarch Abraham, give evidence of highly perfect laws and of a civilization which must have antedated their production by centuries, we gain another yet more emphatic impression of human antiquity Add to all this the palaeontological evidence of man s association with various genera and numerous successive species of prehistoric animals of which he alone survives and the evidence is complete

FUTURE OF HUMANITY

Because of his intelligence and communal co operation man is no longer subject to the laws which govern the adaptation of animals to their environment Osborn's law of adaptive radiation, which as [illegible]

affects his physical frame, while theirs is natural and the stamp of environment is deeply impressed upon the organism

Man's physical evolution has virtually ceased, but in so far as any change is being effected, it is largely retrogressive Such changes are Reduction of hair and teeth, and of hand skill, and dulling of the senses of sight, smell, and hearing upon which active creatures depend so largely for safety That sort of charity which fosters the physically, mentally, and morally feeble, and is thus contrary to the law of natural selection, must also in the long run have an adverse effect upon the race

Man is hardly as yet subject to Malthus law, for while he is increasing more rapidly than any other animal owing largely to the care of the young which makes the expectation of life of the new born relatively very high his migratory ability, but above all his intelligence save him from the application of the law A single new discovery such as that of electricity may increase his food supply and other life necessities several fold His future evolution in so far as it is progressive will be mental and spiritual rather than physical and as such will be the logical conclusion of the marvelous results of organic evolution.

Sinanthropus pekinensis

A remarkable new discovery has come to light during the last few years and deserves to be added to the foregoing account by Professor Lull the discovery of Pekin man *Sinanthropus pekinensis* Next to *Pithecanthropus* in the fossil series of primitive man and only a stage more advanced is this newly discovered genus A few years ago Professor Davidson Black found some fossil teeth near Pekin China which though distinctively human were different enough from any others known to be assigned to a new genus of man Search for further remains in the same neighborhood brought to light two lower jaws containing the kind of teeth discovered by Black The investigation was climaxed a little later when the Chinese anthropologist W C Pei unearthed in the same neighborhood a complete cranium At last reports collectors had brought in parts of skeletons of at least ten individuals While *Sinanthropus* is more like *Pithecanthropus* than any other extinct genus of man it is a more advanced type and helps materially to bridge the gap between *Pithecanthropus* and the higher human genera At this writing further details about this new genus would be inappropriate since investigations upon it are still in progress

CHAPTER XII

EVIDENCES FROM GEOGRAPHIC DISTRIBUTION

PRINCIPLES OF GEOGRAPHIC DISTRIBUTION

Just as palaeontology may be said to be a study of the vertical distribution (distribution in time) of organisms, so geographic distribution may be called a study of the horizontal distribution of organisms, on the earth's surface at any given time (spatial distribution). We are chiefly to be concerned with the *present* spatial distribution of animal and plant species but equally interesting studies have been and still may be made of the horizontal or contemporaneous existence of extinct forms. Much new knowledge has been gained by combining the data of palaeontology with those of geographic distribution. In fact, neither field can be studied profitably without recourse to the other. This fact was clearly perceived by J. A. Thomson in his little manual on *Evolution* when he combined the two types of evidence in one chapter under the title "Evidences of Evolution from Explorer and Palaeontologist."

It was a consideration of the present and of the past distribution of Edentates that led Charles Darwin to his first clear concept of descent with modification. In his voyage on the "Beagle" he found that present day Edentates (armadillos, sloths, anteaters), a very peculiar group of archaic mammals, are practically confined to South America. When he also found that the only fossil Edentates, resembling but also differing from the existing types, are also confined to South America, he easily arrived at the only inference permitted by the facts, that the present Edentates are the modified descendants of the Edentates of the past.

The following quotations from both an older and a recent writer will give the reader a clear idea of the ways in which the general facts of geographic distribution bear witness to the truth of the evolutionary principle.

"The theory," says Wallace,[1] "which we may now take as established—that all the existing forms of life have been derived from other forms by a natural process of descent with modification, and that this same process has been in action during past geological time—should

[1] From A. R. Wallace, *Darwinism* (1889). Used by special permission of the publishers, The Macmillan Company.

enable us to give a rational account not only of the peculiarities of form and structure presented by animals and plants, but also of their grouping together in certain areas, and their general distribution over the earth's surface

"*In the absence of any exact knowledge of the facts of distribution*, a student of the theory of evolution might naturally anticipate that all groups of allied organisms would be found in the same region, and that, as he travelled farther and farther from any given centre, the forms of life would differ more and more from those which prevailed at the starting point, till, in the remotest regions to which he could penetrate, he would find an entirely new assemblage of animals and plants, altogether unlike those with which he was familiar He would also anticipate that diversities of climate would always be associated with a corresponding diversity in the forms of life

"Now these anticipations are to a considerable extent justified Remoteness on the earth's surface is usually an indication of diversity in the fauna and flora, while strongly contrasted climates are always *accompanied by a considerable contrast in the forms of life* But this correspondence is by no means exact or proportionate, and the converse propositions are often quite untrue Countries which are near to each other often differ radically in their animal and vegetable productions, while similarity of climate, together with moderate geographical proximity, are often accompanied by marked diversities in the prevailing forms of life Again, while many groups of animals—genera, families, and sometimes even orders—are confined to limited regions, most of the families, many genera, and even some species are found in every part of the earth An enumeration of a few of these anomalies will better illustrate the nature of the problem we have to solve

"As examples of extreme diversity, notwithstanding geographical proximity, we may adduce Madagascar and Africa, whose animal and vegetable productions are far less alike than are those of Great Britain and Japan at the remotest extremities of the great northern continent, while an equal, or perhaps even a still greater, diversity exists between Australia and New Zealand. On the other hand, Northern Africa and South Europe, though separated by the Mediterranean Sea, have faunas and floras which do not differ from each other more than do the various countries of Europe As a proof that similarity of climate and general adaptability have had but a small part in determining the forms of life in each country, we have the fact of the enormous increase

of rabbits and pigs in Australia and New Zealand of horses and cattle in South America and of the common sparrow in North America though in none of these cases are the animals natives of the countries in which they thrive so well And lastly, in illustration of the fact that allied forms are not always found in adjacent regions we have the tapirs which are found only on opposite sides of the globe in tropical America and the Malayan Islands the camels of the Asiatic deserts whose nearest allies are the llamas and alpacas of the Andes and the marsupials only found in Australia and on the opposite side of the globe in America Yet again although mammalia may be said to be universally distributed over the globe being found abundantly on all the continents and on a great many of the larger islands yet they are entirely wanting in New Zealand, and in a considerable number of other islands which are nevertheless perfectly able to support them when introduced

Now most of these difficulties can be solved by means of well known geographical and geological facts When the productions of remote countries resemble each other there is almost always continuity of land with similarity of climate between them When adjacent countries differ greatly in their productions we find them separated by a sea or strait whose great depth is an indication of its antiquity or permanence When a group of animals inhabits two countries or regions separated by wide oceans it is found that in past geological times the same group was much more widely distributed and may have reached the countries it inhabits from an intermediate region in which it is now extinct We know also that countries now united by land were divided by arms of the sea at a not very remote epoch while there is good reason to believe that others now entirely isolated by a broad expanse of sea were formerly united and formed a single land area There is also another important factor to be taken account of in considering how animals and plants have acquired their present peculiarities of distribution —changes of climate We know that quite recently a glacial epoch extended over much of what are now the temperate regions of the northern hemisphere and that consequently the organisms which inhabit those parts must be comparatively speaking recent immigrants from more southern lands But it is a *yet more important fact that down to middle Tertiary times at all* events an equable temperate climate with a luxuriant vegetation extended to far within the Arctic circle over what are now barren wastes covered for ten months of the year with snow and ice The

Arctic zone has, therefore, been in past times capable of supporting almost all of the forms of life of our temperate regions, and we must take account of this condition of things whenever we have to speculate on the possible migration of organisms between the old and new continents."

"Many of the facts of distribution," says Shull,[1] "are capable of interpretation by the assumption that evolution has operated with the other factors. If each kind of animal has arisen from a pre-existing kind, then each group of related animals must have had an ancestral form, and if the component parts of the groups are widespread the range of the ancestral form may be considered to be the center of dispersal of the group The facts of distribution can apparently be interpreted only on this basis

"Accepting evolution, along with the other factors which can be recognized, the method of distribution is generally conceived to be as follows The ancestral form tends to spread in all directions In some directions it is limited by unfavourable conditions either throughout its life or for some time. In other directions it extends its range Anywhere within its range new types of individuals may arise through the process of evolution These new types may be fitted to occupy new regions, and if they are formed near the limits of the range they may find opportunity to spread into areas which are inaccessible to the unaltered members of the species Thus may arise recognizably distinct forms coincident in range with certain environmental conditions If particular forms, or the individuals of a single form are accidentally (or possibly by sporadic migration) transferred across barriers the distribution of the group becomes discontinuous If these processes have been going on for a long time, that is if the common ancestors of a group of forms existed long ago the range may have had time to become very extensive, or its discontinuity very marked If contrariwise, the ancestors were comparatively recent, the range is likely to be much smaller For this reason groups that have diverged far enough to have attained the rank of families are on the whole more widespread than those so nearly allied as to be considered genera *Should the environment become altered within a* given range, the occupying form might be driven from it or destroyed

[1] From A F Shull *Principles of Animal Biology* (copyright 1920) Used by special permission of the publishers, The McGraw Hill Book Company

If the environment in a region adjoining a range should change in a favourable manner, the range might be extended at that point without any alteration on the part of the animals

"The distribution of animals is inferred to be in harmony with this method, which involves, it will be noted, the factors of migration, evolution, physiological and morphological dependence upon the environment, the diversity and changeableness of the earth's surface, and extinction, and in this manner are explained the differences in geographical position differences in size of range, differences in the continuity of range and the fact that ranges are at first continuous, differences in physical and biological conditions which characterize the ranges of different forms and the geographical proximity of apparently related forms"

SOME OF THE MORE SIGNIFICANT FACTS ABOUT THE DISTRIBUTION OF ANIMALS

THE FAUNA OF OCEANIC ISLANDS[1]

GEORGE JOHN ROMANES

Turning now from aquatic organisms to terrestrial, the body of facts from which to draw is so large, that I think the space at my disposal may be best utilized by confining attention to a single division of them—that, namely, which is furnished by the zoological study of oceanic islands

In the comparatively limited—but in itself extensive—class of facts thus presented, we have a particularly fair and cogent test as between the alternative theories of evolution and creation For where we meet with a volcanic island, hundreds of miles from any other land, and rising abruptly from an ocean of enormous depth, we may be quite sure that such an island can never have formed part of a now submerged continent In other words, we may be quite sure that it always has been what it now is—an oceanic peak, separated from all other land by hundreds of miles of sea, and therefore an area supplied by nature for the purpose as it were, of testing the rival theories of creation and evolution For let us ask, upon these tiny insular specks of land what kind of life should we expect to find? To this question the theories of special creation and of gradual evolution would agree in giving the same answer up to a certain point For both theories would agree in supposing that these islands would at all

[1] From G J Romanes *Darwin and after Darwin* (copyright 1892) Used by special permission of The Open Court Publishing Company

events in large part derive their inhabitants from accidental or occasional arrivals of wind blown or water floated organisms from other countries—especially, of course, from the countries least remote But after agreeing upon this point, the two theories must part company in their anticipations The special creation theory can have no reason to suppose that a small volcanic island in the midst of a great ocean should be chosen as the theatre of any extraordinary creative activity or for any particularly rich manufacture of peculiar species to be found nowhere else in the world On the other hand, the evolution theory would expect to find that such habitats are stocked with more or less peculiar species For it would expect that when any organisms chanced to reach a wholly isolated refuge of this kind their descendants should forthwith have started upon an independent course of evolutionary history Protected from intercrossing with any members of their parent species elsewhere, and exposed to considerable changes in their conditions of life, it would indeed be fatal to the general theory of evolution if these descendants, during the course of many generations, were not to undergo appreciable change It has happened on two or three occasions that European rats have been accidentally imported by ships upon some of these islands and even already it is observed that their descendants have undergone a slight change of appearance, so as to constitute them what naturalists call local varieties The change, of course is but slight because the time allowed for it has been so short But the longer the time that a colony of a species is thus completely isolated under changed conditions of life the greater, according to the evolution theory, should we expect the change to become Therefore in all cases where we happen to know, from independent evidence of a geological kind, that an oceanic island is of very ancient formation the evolution theory would expect to encounter a great wealth of peculiar species On the other hand, as I have just observed the special creation theory can have no reason to suppose that there should be any correlation between the age of an oceanic island and the number of peculiar species which it may be found to contain

Therefore having considered the principles of geographical distribution from the widest or most general point of view we shall pass to the opposite extreme and consider exhaustively, or in the utmost possible detail the facts of such distribution where the conditions are best suited to this purpose—that is, as I have already said, upon oceanic islands which may be metaphorically regarded as having been

formed by nature for the particular purpose of supplying naturalists with a crucial test between the theories of creation and evolution The material upon which my analysis is to be based will be derived from the most recent works upon geographical distribution—especially from the magnificent contributions to this department of science which we owe to the labours of Mr Wallace Indeed, all that follows may be regarded as a condensed filtrate of the facts which he has collected Even as thus restricted, however, our subject matter would be too extensive to be dealt with on the present occasion were we to attempt an exhaustive analysis of the floras and faunas of all oceanic islands upon the face of the globe Therefore, what I propose to do is to select for such exhaustive analysis a few of what may be termed the most oceanic of oceanic islands—that is to say, those oceanic islands which are most widely separated from main lands, and which therefore, furnish the most unquestionable of test cases as between the theories of special creation and genetic descent

Azores—A group of volcanic islands, nine in number, about 900 miles from the coast of Portugal and surrounded by ocean depths of 1 800 to 2,500 fathoms There is geological evidence that the origin of the group dates back at least as far as Miocene times There is a total absence of all terrestrial Vertebrata, other than those which are known to have been introduced by man Flying animals, on the other hand, are abundant namely, 53 species of birds, one species of bat, a few species of butterflies, moths and hymenoptera, with 74 species of indigenous beetles All these animals are unmodified European species with the exception of one bird and many of the beetles Of the 74 indigenous species of the latter, 36 are not found in Europe, but 19 are natives of Madeira or the Canaries, and 3 are American, doubtless transplanted by drift wood The remaining 14 species occur nowhere else in the world, though for the most part they are allied to other European species There are 69 known species of land shells, of which 37 are European, and 32 peculiar though all allied to European forms Lastly, there are 480 known species of plants of which 40 are peculiar, though allied to European species

Bermudas.—A small volcanic group of islands, 700 miles from North Carolina. Athough there are about 100 islands in the group, their total area does not exceed 50 square miles The group is surrounded by water varying in depth from 2,500 to 3,800 fathoms The

only terrestrial Vertebrate (unless the rats and mice are indigenous) is a lizard allied to an American form, but specifically distinct from it and therefore a solitary species which does not occur anywhere else in the world None of the birds or bats are peculiar, any more than in the case of the Azores, but, as in that case, a large percentage of the land shells are so—namely, at least one quarter of the whole Neither the botany nor the entomology of this group has been worked out but I have said enough to show how remarkably parallel are the cases of these two volcanic groups of islands situated in different hemispheres but at about the same distance from large continents In both there is an extraordinary paucity of terrestrial Vertebrata, and of any peculiar species of bird or beast On the other hand, there is in both a marvellous wealth of peculiar species of insects and land shells Now these correlations are all abundantly intelligible It is a difficult matter for any terrestrial animal to cross 900, or even 700 miles of ocean therefore only one lizard has succeeded in doing so in one of the two parallel cases, and living cut off from intercrossing with its parent form, the descendants of that lizard have become modified so as to constitute a peculiar species. But it is more easy for large flying animals to cross those distances of ocean consequently, there is only one instance of a peculiar species of bird or bat—namely, a bull finch in the Azores which being a small land bird, is not likely ever to have had any other visitors from its original parent species coming over from Europe to keep up the original breed Lastly, it is very much more easy for insects and land mollusca to be conveyed to such islands by wind and floating timber than it is for terrestrial mammals, or even than it is for small birds and bats but yet such means of transit are not sufficiently sure to admit of much recruiting from the mainland for the purpose of keeping up the specific types. Consequently, the insects and the land shells present a much greater proportion of peculiar species—namely, one half and one fourth of the land shells in the one case, and one eighth of the beetles in the other All these correlations, I say, are abundantly intelligible on the theory of evolution but who shall explain, on the opposite theory, why orders of beetles and land mollusca should have been chosen from among all other animals for such superabundant creation on oceanic islands, so that in the Azores alone we find no less than 32 of the one and 14 of the other? And, in this connection, I may again allude to the peculiar species of beetles in the island of Madeira Here there are an enormous *number of peculiar species, though they are nearly all related to*

or included under the same genera as beetles on the neighboring continent Now, as we have previously seen, no less than 200 of these species have lost the use of their wings Evolutionists explain this remarkable fact by their general laws of degeneration under disuse, and the operation of natural selection as will be shown later on, but it is not so easy for special creationists to explain why this enormous number of peculiar species of beetles should have been deposited on Madeira all allied to beetles on the nearest continent, and nearly all deprived of the use of their wings And similarly of course, with all the peculiar species of the Bermudas and the Azores For who will explain, on the theory of independent creation, why all the peculiar species both of animals and plants, which occur on the Bermudas should so unmistakably present American affinities while those which occur on the Azores no less unmistakably present European affinities? But to proceed to other and still more remarkable, cases

The Galapagos Islands —This archipelago is of volcanic origin, situated under the equator between 500 and 600 miles from the West Coast of South America The depth of the ocean around them varies from 2 000 to 3,000 fathoms or more This group is of peculiar interest from the fact that it was the study of its fauna which first suggested to Darwin s mind the theory of evolution I will therefore begin by quoting a short passage from his writings upon the zoological relations of this particular fauna

"Here almost every product of the land and of the water bears the unmistakable stamp of the American continent There are twenty-six land birds, of these, twenty one, or perhaps twenty three, are ranked as distinct species, and would commonly be assumed to have been here created, yet the close affinity of most of these birds to American species is manifest in every character, in their habits, gestures and tones of voice So it is with the other animals and with a large proportion of the plants, as shown by Dr Hooker in his admirable Flora of this archipelago The naturalist, looking at the inhabitants of these volcanic islands in the Pacific, distant several hundred miles from the continent, feels that he is standing on American land. Why should this be so? Why should the species which are supposed to have been created in the Galapagos Archipelago, and nowhere else, bear so plainly the stamp of affinity to those created in America? There is nothing in the conditions of life, in the geological nature of the islands, in their height or climate, or in the proportions in which the several classes are associated together, which closely resembles the

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more restricted range and therefore the least likely to have found their way to the islands with any frequency

The insect fauna of the Galapagos Islands is scanty, and chiefly composed of beetles These number 35 species which are nearly all peculiar and in some cases go to constitute peculiar genera The same remarks apply to the twenty species of land-shells Lastly, of the total number of flowering plants (332 species) more than one half (174 species) are peculiar It is observable in the case of these peculiar species of plants—as also of the peculiar species of birds—that many of them are restricted to single islands It is also observable that with regard both to the fauna and flora the Galapagos Islands as a whole are very much richer in peculiar species than either the Azores or Bermudas notwithstanding that both the latter are considerably more remote from the nearest continents This difference, which at first sight appears to make against the evolutionary interpretation really tends to confirm it For the Galapagos Islands are situated in a calm region of the globe unvisited by those periodic storms and hurricanes which sweep over the North Atlantic and which every year convey some straggling birds insects seeds etc, to the Azores and Bermudas Notwithstanding their somewhat greater isolation geographically therefore, the Azores and Bermudas are really less isolated biologically than are the Galapagos Islands, and hence the less degree of peculiarity on the part of their endemic species But on the theory of special creation, it is impossible to understand why there should be any such correlation between the prevalence of gales and a comparative inertness of creative activity And, as we have seen it is equally impossible on this theory to understand why there should be a further correlation between the *degree* of peculiarity on the part of the isolated species, and the *degree* in which their nearest allies on the mainland are there confined to narrow ranges, and therefore less likely to keep up any biological communication with the islands.

St. Helena —A small volcanic island, ten miles long by eight wide, situated in mid-ocean, 1,100 miles from Africa, and 1,800 from South America It is very mountainous and rugged, bounded for the most part by precipices, rising from ocean depths of 17,000 feet, to a height above the sea level of nearly 3 000 When first discovered it was richly clothed with forests, but these were all destroyed by human agency during the 16th 17th and 18th centuries The records of civilization present no more lamentable instance of this kind of destruction

from a merely pecuniary point of view the abolition of these primeval forests has proved an irreparable loss, but from a scientific point of view the loss is incalculable These forests served to harbour countless forms of life, which extended at least from the Miocene age and which, having found there an ocean refuge survived as the last remnants of a remote geological epoch In those days, as Mr Wallace observes St Helena must have formed a kind of natural museum or vivarium of archaic species of all classes, the interest of which we can now only surmise from the few remnants of those remnants, which are still left among the more inaccessible portions of the mountain peaks and crater edges These remnants of remnants are as follows

There is a total absence of all indigenous mammals reptiles fresh water fish, and true land birds. There is however a species of plover, allied to one in South Africa but it is specifically distinct and therefore peculiar to the island The insect life on the other hand is abundant. Of beetles, no less than 129 species are believed to be aboriginal, and, with one single exception the whole number are peculiar to the island 'But in addition to this large amount of specific peculiarity (perhaps unequalled anywhere else in the world) the beetles of this island are remarkable for their generic isolation, and for the altogether exceptional proportion in which the great divisions of the order are represented The species belong to 39 genera, of which no less than 25 are peculiar to the island, and many of these are such isolated forms that it is impossible to find their allies in any particular country ' [Wallace] More than two thirds of all the species belong to one group of weevils—a circumstance which serves to explain the great wealth of beetle-population the weevils being beetles which live in wood, and St Helena having been originally a densely wooded island This circumstance is also in accordance with the view that the peculiar insect fauna has been in large part evolved from ancestors which reached the island by means of floating timber for of course no explanation can be suggested why special creation of this highly peculiar insect fauna should have run so disproportionately into the production of weevils About two-thirds of the whole number of beetles or over 80 species show no close affinity with any existing insects, while the remaining third have some relations, though often very remote, with European and African forms That this high degree of peculiarity is due to high antiquity is further indicated according to our theory by the large number of species which some of the types comprise Thus, the 54 species of *Cossonidae* may be

referred to three types the 11 species of *Bembidium* form a group by themselves, and the *Heteromera* form two groups "Now, each of these types may well be descended from a single species, which originally reached the island from some other land, and the great variety of generic and specific forms into which some of them have diverged is an indication, and to some extent a measure, of the remoteness of their origin" [Wallace] But on the counter supposition that all these 128 peculiar species were separately created to occupy this particular island, it is surely unaccountable that they should thus present such an arborescence of natural affinities amongst themselves

Passing over the rest of the insect fauna, which has not yet been sufficiently worked out, we next find that there are only 20 species of indigenous land shells—which is not surprising when we remember by what enormous reaches of ocean the land is surrounded Of these 20 species no less than 13 have become extinct three are allied to European species while the rest are so highly peculiar as to have no near allies in any other part of the globe So that the land shells tell exactly the same story as the insects

Lastly, the plants likewise tell the same story The truly indigenous flowering plants are about 50 in number, besides 26 ferns Forty of the former and ten of the latter are peculiar to the island and, as Sir Joseph Hooker tells us, ' cannot be regarded as very close specific allies of any other plants at all " Seventeen of them belong to peculiar genera, and the others all differ so markedly as species from their congeners, that not one comes under the category of being an insular form of a continental species So that with respect to its plants, no less than with respect to its animals, we find that the island of St Helena constitutes a little world of unique species, allied among themselves, but diverging so much from all other known forms that in many cases they constitute unique genera

Sandwich Islands—*These are an extensive group of islands*, larger than any we have hitherto considered—the largest of the group being about the size of Devonshire The entire archipelago is volcanic, with mountains rising to a height of nearly 14 000 feet The group is situated in the middle of the North Pacific at a distance of considerably over 2,000 miles from any other land and surrounded by enormous ocean depths The only terrestrial vertebrates are two lizards, one of which constitutes a peculiar genus There are 24 aquatic birds, five of which are peculiar, four birds of prey, two of which are peculiar, and 16 land birds, all of which are peculiar

Moreover, these 16 land birds constitute no less than 10 peculiar genera, and even one peculiar family of five genera This is an amount of peculiarity far exceeding that of any other islands, and, of course, corresponds with the great isolation of this archipelago The only other animals which have here been carefully studied are the land shells, and these tell the same story as the birds For there are no less than 400 species which are all, without any exception, peculiar, while about three-quarters of them go to constitute peculiar genera Again, of the plants, 620 species are believed to be endemic, and of these 377 are peculiar, yielding no less than 39 peculiar genera

THE FAUNA OF CONTINENTAL ISLANDS—MADAGASCAR AND NEW ZEALAND[1]

A. R. WALLACE

The two exceptions just referred to are Madagascar and New Zealand, and all the evidence goes to show that in these cases the land connection with the nearest continental area was very remote in time The extraordinary isolation of the productions of Madagascar—almost all the most characteristic forms of mammalia, birds, and reptiles of Africa being absent from it—renders it certain that it must have been separated from that continent very early in the Tertiary, if not as far back as the latter part of the Secondary period, and this extreme antiquity is indicated by a depth of considerably more than a thousand fathoms in the Mozambique Channel, though this deep portion is less than a hundred miles wide between the Comoro Islands and the main land Madagascar is the only island on the globe with a fairly rich mammalian fauna which is separated from a continent by a depth greater than a thousand fathoms, and no other island presents so many peculiarities in these animals, or has preserved so many lowly organised and archaic forms The exceptional character of its productions agrees exactly with its exceptional isolation by means of a very deep arm of the sea

New Zealand possesses no known mammals and only a single species of batrachian, but its geological structure is perfectly continental There is also much evidence that it does possess one mammal, although no specimens have been yet obtained Its reptiles and birds are highly peculiar and more numerous than in any truly oceanic island Now the sea which directly separates New Zealand from Australia is more than 2,000 fathoms deep, but in a north west direc

[1] From A R Wallace, *Darwinism* (copyright 1889) Used by special permission of the publishers The Macmillan Company

tion there is an extensive bank under 1,000 fathoms, extending to and including Lord Howe's Island, while north of this are other banks of the same depth, approaching towards a submarine extension of Queensland on the one hand, and New Caledonia on the other, and altogether suggestive of a land union with Australia at some very remote period Now the peculiar relations of the New Zealand fauna and flora with those of Australia and of the tropical Pacific Islands to the northward indicate such a connection, probably during the Cretaceous period and here, again, we have the exceptional depth of the dividing sea and the form of the ocean bottom according well with the altogether exceptional isolation of New Zealand, an isolation which has been held by some naturalists to be great enough to justify its claim to be one of the primary Zoological Regions

THE DISTRIBUTION OF MARSUPIALS[1]

A R WALLACE

This singular and lowly organised type of mammals constitutes almost the sole representative of the class in Australia and New Guinea while it is entirely unknown in Asia, Africa, or Europe It reappears in America, where several species of opossums are found, and it was long thought necessary to postulate a direct southern connection of these distant countries, in order to account for this curious fact of distribution. When, however, we look to what is known of the geological history of the marsupials the difficulty vanishes In the Upper Eocene deposits of Western Europe the remains of several animals closely allied to the American opossums have been found and as, at this period, a very mild climate prevailed far up into the arctic regions, there is no difficulty in supposing that the ancestors of the group entered America from Europe or Northern Asia during early Tertiary times

But we must go much further back for the origin of the Australian marsupials All the chief types of the higher mammalia were in existence in the Eocene, if not in the preceding Cretaceous period and as we find none of these in Australia, that country must have been finally separated from the Asiatic continent during the Secondary or Mesozoic period Now during that period, in the Upper and the Lower Oolite and in the still older Trias the jaw-bones of numerous small mammalia have been found, forming eight distinct genera, which

[1] From A. R. Wallace *Darwinism* (copyright 1889) Used by special permission of the publishers, The Macmillan Company

are believed to have been either marsupials or some allied lowly forms In North America also, in beds of the Jurassic and Triassic formations, the remains of an equally great variety of these small mammalia have been discovered, and from the examination of more than sixty specimens, belonging to at least six distinct genera, Professor Marsh is of the opinion that they represent a generalised type, from which the more specialised marsupials and insectivora were developed

From the fact that very similar mammals occur both in Europe and America at corresponding periods and in beds which represent a long succession of geological time, and that during the whole of this time no fragments of any higher forms have been discovered, it seems probable that both the northern continents (or the larger portion of their area) were then inhabited by no other mammalia than these, with perhaps other equally low types It was, probably, not later than the Jurassic age when some of these primitive marsupials were able to enter Australia, where they have since remained almost completely isolated, and, being free from the competition of higher forms, they have developed into the great variety of types we now behold there These occupy the place and have to some extent acquired the form and structure of distinct orders of the higher mammals—the rodents, the insectivora and the carnivora—while still preserving the essential characteristics and lowly organisation of the marsupials At a much later period—probably in late Tertiary times—the ancestors of the various species of rats and mice which now abound in Australia and which, with the aerial bats, constitute its only forms of placental mammals, entered the country from some of the adjacent islands For this purpose a land connection was not necessary, as these small creatures might easily be conveyed among the branches or in the crevices of trees uprooted by floods and carried down to the sea, and then floated to a shore many miles distant That no actual land connection with or very close approximation to, an Asiatic island had occurred in recent times is sufficiently proved by the fact that no squirrel, pig civet or other widespread mammal of the Eastern hemisphere has been able to reach the Australian continent

THE DISTRIBUTION OF BIRDS

A. R WALLACE

These vary much in their powers of flight, and their capability of traversing wide seas and oceans Many swimming and wading birds

[1] From A R Wallace *Darwinism* (copyright 1891) Used by special permission of the publishers The Macmillan Company

can continue long on the wing, fly swiftly, and have, besides, the power of resting safely on the surface of the water These would hardly be limited by any width of ocean, except for the need of food and many of them, as the gulls, petrels and divers find abundance of food on the surface of the sea itself These groups have a wide distribution *across* the oceans while waders—especially plovers, sandpipers snipes, and herons—are equally cosmopolitan, travelling *along* the coasts of all the continents and across the narrow seas which separate them Many of these birds seem unaffected by climate, and as the organisms on which they feed are especially abundant on arctic, temperate and tropical shores there is hardly any limit to the range even of some of the species

Land birds are much more restricted in their range, owing to their usually limited powers of flight their inability to rest on the surface of the sea or to obtain food from it, and their greater specialisation, which renders them less able to maintain themselves in the new countries they may occasionally reach Many of them are adapted to live only in woods or in marshes or in deserts, they need particular kinds of food or a limited range of temperature, and they are adapted to cope only with the special enemies or the particular group of competitors among which they have been developed Such birds as these may pass again and again to a new country, but are never able to establish themselves in it and it is this organic barrier, as it is termed rather than any physical barrier, which, in many cases, determines the presence of a species in one area and its absence from another We must always remember, therefore, that, although the presence of a species in a remote oceanic island clearly proves that its ancestors must at one time have found their way there, the absence of a species does not prove the contrary, since it also may have reached the island but have been unable to maintain itself, owing to the inorganic or organic conditions not being suitable to it This general principle applies to all classes of organisms and there are many striking illustrations of it In the Azores there are eighteen species of land birds which are permanent residents, but there are also several others which reach the islands almost every year after great storms, but have never been able to establish themselves In Bermuda the facts are still more striking, since there are only ten species of resident birds, while no less than twenty other species of land birds and more than a hundred species of waders and aquatics are frequent visitors, often in great numbers, but are never able to establish themselves

SUMMARY OF MAMMALIAN DISPERSAL[1]

HANS GADOW

Australia as the earliest great mass of land permanently severed from the rest is in almost undisturbed possession of the lowest mammals It is the sole refuge of the monotremes, and the marsupials have narrowly escaped a similar fate They take us to the next independent continent, South America This had three chances, or epochs of being stocked with mammals Within the Cretaceous period it seems to have received its marsupial stock from the north, the progenitors of all modern marsupials A second influx during the early Tertiary brought edentates and rodents as its first Placentals from Africa, and those queer Ungulates, the Toxodonts and Pyrotheria unless we prefer to look upon these Eocene extinct orders as truly aboriginal to South America, when this was still continuous with the ancient Brazil Afro-Indian Gondwanaland The third and last inroad came once more from the north, when with the close of the Miocene permanent connection with North America was re-established This brought the modern odd toed and pair toed Ungulates, with dogs cats and bears in their wake, and lastly man

There remains the huge North World Eurasia and North America have always formed a wide circumpolar ring, which repeatedly broke and joined again Whatever group of terrestrial creatures was developed in the eastern, Asiatic, half, was sure to turn up in the western, and vice versa

Lastly, the mysterious African continent It began originally as the centre of the ancient equatorial South World, it has lost these connections and has become joined to the northland after many vicissitudes It is therefore most difficult to apportion its fauna rightly moreover for fossils it is almost a blank, except Egypt. It must have had some share in the evolution of mammals, like edentates, rodents insectivores, hyrax, elephants, sirenians and lemurs, all groups with an ancient stamp But what share it had against Eurasia, in the development of say ungulates, carnivores, monkeys, we do not know Not much is likely to have originated in Europe, the elephants, rhinos, hippos, lions and hyaenas were migrants rather from than to Africa, rarely across some Mediterranean bridge, usually by Asia Minor

The more dominant forms of our present fauna have originated, to use an expression of Darwin's, "in the larger areas and more efficient

[1] From Hans Gadow, *Wanderings of Animals* (1913) Cambridge University Press.

workshops of the north," and the balance is in favour of Asia as the cradle of modern mammals

Is it an idle dream to think of the future? A survey of the past reveals the vanishing of whole faunas from extensive countries, which were then repeopled by other forms from elsewhere What has happened before, may happen in times to come Countless groups, once flourishing, are no more, many others have had their day and are now on the decline, whilst others are flourishing now, are even in the increase and seem to have a future before them Such favoured assemblies are the toads and frogs, lizards and snakes, Passerine birds and rodents, mostly the small sized members of their tribes, the days of giants are past All this has happened in the natural course of events, without the influence of man, who only within most recent times has become the most potent and destructive factor to the ancient faunas of the world

SUMMARY OF THE ARGUMENT FOR EVOLUTION AS BASED ON GEOGRAPHIC DISTRIBUTION

On the hypothesis of special creation or on any other hypothesis except evolution that has even been suggested, the extremely intricate patchwork of animal and plant distribution remains an unsolvable picture puzzle without rhyme or reason When this puzzle is attacked with the aid of the evolutionary idea, the key to the whole maze is furnished and the difficulties clear up with remarkable ease The whole hodgepodge makes sense and we can understand many previously irreconcilable facts In no field does the working hypothesis of evolution work to such advantage as in this field

On the basis that a species arises at one place, spreads out over large areas, becoming modified as it goes, that new species are formed from old through modification after isolation from the parent-stock, how do the facts of distribution look when examined in detail?

1 Cosmopolitan groups, those with the widest distribution, are those to whom no barriers are sufficient to check migration, e g, strong fliers, Man, earthworms carried by Man

2 Restricted groups are usually those to which barriers are readily set up and are frequently the last remnants of a formerly successful fauna or flora, which continue to survive only in some restricted area where the conditions are rather more favorable than elsewhere

3 The study of the distribution of species belonging to a single genus reveals that the more primitive or generalized species occupy a central position and the most specialized species are at the outer boundaries of the distributional area

4 The faunas and floras of continental islands are just what we should expect on the basis that there was at one time a land connection with the nearest continent that at this time the faunas and floras were the same on both island and continent that later the continent and island were separated by an impassable barrier of ocean and that the inhabitants of the two bodies evolved separately

5 The faunas and floras of oceanic islands are like those of the nearest mainland and are of those types for the most part that might most readily have been blown there by the wind or carried on floating debris

6 The conclusions arrived at by students of geographic distribution past and present as to the existence of former land connections now broken are borne out by the independent findings of geologists and geographers.

PART III

THE MECHANISM OF EVOLUTION (GENETICS)

CHAPTER XIII

INTRODUCTORY STATEMENT

THE NATURE AND SCOPE OF GENETICS

The validity of the general principle of evolution rests on the kind of evidence presented in previous chapters Volumes could be written giving further evidence of the same sort. Very few thoughtful persons once confronted with these evidences fail to be convinced as to the reality of evolution

It is one thing to know that evolution has occurred and has followed certain courses but quite another thing to understand what forces underly the process A going process must have causes and it is our purpose in this section of the course to present an account of what we know or what we think we know about the causes of organic evolution

Our method of study is one that depends on the validity of the doctrine of uniformitarianism Exactly as in the science of geology the method of investigation is that of studying in detail the changes going on today of assuming that present changes are of the same nature as changes in the past and that the past may be interpreted in terms of what we discover about the present Thus long series of generations of rapidly breeding animals and plants are studied intensively over periods of years some species having been bred for over twenty five years or for at least seven hundred generations a period equivalent in number of generations to 25 000 years of human life Hundreds of millions of individuals have been passed in review before the keenly trained eyes of an army of competent investigators all on the lookout for the slightest change from the normal Any observed change is then followed through subsequent generations to determine whether it is hereditary and how it affects the success of individuals possessing it Studies of this sort together with examinations of the germ cells to see whether or not correlated changes have occurred in their materials and mathematical calculations of the relative frequencies with which different characters occur in combination with one another have led to an understanding of the mechanism of evolution far more complete and detailed than anyone a decade or so ago could possibly have hoped to attain

The experimental and analytical study of the processes and mech

anisms of evolution is the province of that branch of evolutionary biology known as *Genetics*

Three principal methods of attack upon the problems of genetics are as follows

a) **Experimental breeding** —This method first carried out systematically by Mendel consists of breeding together two individuals differing in certain well defined characters and of determining the ratios in which the contrasting parental characters reappear in successive generations of descendants Mendel s method has been extremely fruitful and in connection with the second method that of cytology has thrown a flood of light on the actual workings of the mechanisms of evolution

b) **Cytology** —This method involves the microscopic study of the germ cells especially during the period of reproduction The observed changes that go on in connection with sexual reproduction have been found to constitute a mechanism adequate to explain the peculiar hereditary regularities constituting Mendel s laws of heredity Also it has been found that most aberrations in heredity are associated with correlated aberrations in the mechanism of reproduction Experimental breeding and cytology have been most intimate and successful collaborators

c) **Statistical analysis** —While experimental breeding and cytology lay stress upon the type of change or the mode of heredity in individuals statistical methods deal chiefly with group changes and with the characteristics of populations Often evolutionary trends or group changes quite undetectable in separate individuals can be detected by statistical methods Also the statistical consequences of a certain type of change in a few or many individuals can be predicted for any given number of generations While the methods of statistical analysis are as a rule too difficult for any but the expert they are becoming more and more essential as a part of the technique of genetics

d) **Observations of changes going on in nature** —Attempts are made to discover evidences of changes in nature equivalent to those observed in the laboratory and there is now considerable evidence favoring the conclusion that laboratory observations are reliable criteria of what takes place in nature

PREREQUISITES FOR THE STUDY OF GENETICS

In order profitably to pursue the study of genetics one must first understand the fundamentals of biology in general for the mechanism

of evolution is largely within the living organism itself One must be familiar with the units of life cells organisms generations One must understand the methods of reproduction and the mechanisms of heredity and variation resident in the cellular components of the organism Also one must never forget that organisms live and grow and reproduce only if in an appropriate environment and that the environment has much to do with the expression of hereditary characters In addition the environment acts as a guiding factor directing the course of evolution along lines of fitness or adaption The highly varied character of the environment, moreover tends to favor a high degree of diversity in organisms and thus to give rise to a vast multiplicity of different types

In view of all this it will be necessary for the general student who has had no previous training in biology to learn the fundamentals of this subject before proceeding with the more specific materials of genetics.

THE MECHANISM OF EVOLUTION

At the beginning of the present century very little was known about the actual mechanism of evolution We had Darwin s theory of natural selection Weismann s theory of germinal continuity and a statistical knowledge of certain aspects of variation and heredity Something was known about the rôle of isolation in species-forming and the general fact of orthogenesis was appreciated With the rediscovery in 1900 of Mendel s work and the announcement by De Vries of the mutation theory genetics really began Thirty odd years of intensive research by hundreds of specialists have contributed so much to our understanding of the workings of evolution that we now consider that we know something about the main causes of evolution

Evolution is now looked upon as an extremely complicated process There is no one cause of evolution as the extreme proponents of natural selection once held rather there are many causes each acting upon and in co-ordination with all the others The mechanism of evolution is like an intricate piece of machinery manufacturing a complex product Each part is geared up with other parts Some parts are concerned with feeding in the raw materials others with separating and distributing the raw materials others with assembling and shaping up the various parts into something useful and with discarding defective and useless parts and still others with sorting out the different kinds of products and keeping them in separate lots

No man made mechanism is so intricate as is the mechanism of evolution, for all man made machines are designed to turn out uniform products, while the evolution machine is especially adapted to turn out highly diverse products

Although we recognize that none of the causal factors of evolution are independent, it makes for clearness of exposition to subdivide the complex machine into five separate factors, each in itself complex enough for further subdivision

THE MAIN CAUSAL FACTORS OF EVOLUTION

I Persistence factors —Under this head are included all agents that make for persistence of type in organisms, resulting in relative constancy of form and function over long periods of time When characters persist unchanged from generation to generation, they are said to be hereditary It is part of our plan to find out what parts of the mechanism promote constancy of type Some of the principal reasons for this constancy are the following

a) The relative stability of the unit materials of heredity, the *genes*
b) The relative constancy of bundles of genes, the *chromosomes*
c) The relative constancy and perfection of operation of the mechanism of *mitotic cell division*, a mechanism that aids in maintaining the constancy of (a) and (b)
d) The relative constancy of the principal factors of the environment over long periods of time

II. Diversity factors —"Diversity" may be defined as variety without the introduction of anything definitely new It involves, first the kaleidoscopic recombination of all the various hereditary unit characters without any change in the unit characters themselves, and, second, the almost equally varied expression of characters under the influence of a highly variable and diversified environment

The chief agent in promoting diversity of combinations is sexual, or gametic, reproduction And the specific mechanisms involved are the mechanisms of *meiosis* and *fertilization*, which are later to be described in detail

The recombinations of unit characters while apparently random in individual cases, give constant statistical ratios that are known as "Mendelian ratios" Mendel s Laws of heredity in general are, in fact, the laws of the random assortment and recombination of unit characters through the instrumentality of meiosis and fertilization

Much of the endless diversity of living beings is, however, not hereditary at all, but is due to variations in the environment The differences in the sizes of beans on a single bean plant, for example, are purely environmental in origin, as experiments have shown, and not in the least hereditary

III Change factors —Change in contrast with diversity, involves the introduction of new unit characters or new gene arrangements It is as though a new piece of colored glass were added to those already present in the kaleidoscope, or a piece of a different color substituted for an old piece, thus changing all future patterns Such changes re sult from the rare modification of individual genes, from equally rare changes in the number of chromosomes, and from the shifting of groups of genes within a chromosome or from one chromosome to another The mechanisms involved are

a) Gene mutations

b) Slips in the regularity of mitosis involving irregularities in the relatively constant operations of heredity The result is a change in the number of chromosomes Several kinds of such irregularities are known and all are called *chromosomal aberrations*

c) Breaks in chromosomes, followed by the reunion of the broken pieces in various new arrangements Such changes are known as *translocations*

d) While most of the changes under (*a*), (*b*), and (*c*) seem to occur spontaneously, there is some evidence that they may have en vironmental causes Hence the environment may be the ulti mate change factor

IV Guiding factors —Evolution has been for the most part order ly, especially in two respects (*a*) The best known fossil pedigrees indicate that changes from age to age tend to follow certain definite trends We have previously spoken of this phenomenon as *ortho genesis* (*b*) Evolutionary changes have also been, at least to a large extent, *adaptive* Most changes have been appropriate to changes in the environment

The chief guiding factor commonly held responsible for both orthogenesis and adaptation is *natural selection* a causal factor of great importance that will be discussed critically in its proper place

Various mystical guiding factors such as Driesch s "*enteleche*" and Bergson s ' *élan vital* " have been posited to account for the apparent

purposiveness of evolution but there is little evidence for the existence of such factors

Lamarck s theory of the *inheritance of acquired characters* was also designed to explain the adaptive character of evolutionary change but there are many reasons for doubting the validity of this theory

V Dividing factors —One of the most striking features of living organisms is their multiplicity of different kinds phyla classes orders families genera species and varieties Evolution has involved the subdividing of old types into numbers of new ones The whole process has been one of the branching out into numerous diverging lines of descent All those agencies that promote the splitting of all old species into two or more new ones are classed as isolation factors There are many means of isolating portions of a species from other portions of the same species These may for convenience be called

a) Geographic isolation
b) Reproductive isolation
c) Psychic isolation
d) Environmental isolation

In general any agent that prevents a particular variant of a species from breeding with the more typical members of that species tends to help to establish the variant type and aids in the production of a distinct new variety species or genus depending on the degree of completeness of isolation and the length of time involved

All of these factors are necessary agents in bringing about the kind of evolution that we know has occurred With perfect heredity and no diversity or change factors the organic world would be at a standstill Successive generations would be exact duplicates of one another Offspring would be exactly like their parents and no evolution would be possible The diversity and change factors without the conserving factor heredity would produce nothing but chaos Two successive generations would be utterly unrelated offspring would be nothing like their parents and change would merely run riot With the heredity diversity and change mechanisms operating as they are known to do but without any guiding factor living things would be little more than a chaotic collection of monstrosities unfit and ill assorted With all the other factors operating as they are known to do but with no dividing factor evolution would proceed along but one front line of advance There would be no multiplicity of groups no system of

branching relationships Thus it is obvious that the factors of evolution are to be conceived of not as independent mechanisms but as interdependent parts of one grand mechanism

It is our purpose to discuss in detail the various component factors of the mechanism of evolution approximately in the order in which they have been listed in this outline

CHAPTER XIV

THE BIOLOGICAL BACKGROUND OF GENETICS

RACES AND INDIVIDUALS

Evolution is racial change In order that a race may change the individuals comprising the race must in large numbers exhibit changed conditions One or a few individuals changing in some peculiar way may not at all affect the status of the species as a whole It is well, then, to remember that true evolutionary changes are mass changes involving whole populations through successive generations A race or a species is to be looked upon as a vast unit continuous in time and space The members of a race are all descended from common ancestors and are interbreeding in all sorts of ways If one should work out a diagram of the genetic relationships of the members of a large species such a diagram of connecting lines of relationship would constitute an almost solid mass of interlacing lines An intricately interconnected group of individuals constituting a race is then a true evolutionary unit Just as cells are the structural units of life, so races are the *evolutionary units* of life Let us now briefly examine the constitution of a race

At any given period of time a race consists of a large group of individuals Some of these are related as parents and offspring others as brothers and sisters others as cousins of varying grades, and all doubtless trace back to some common ancestors a score of generations ago The individuals constituting the race at one period are not at all the same individuals that constituted that race a few years previously and none of them will be represented in that race a few years hence Individuals, then are temporary components of the race, but the race itself is permanent and relatively constant, though slowly changing as a whole

It is our problem to determine the relation of the individual to the race and to account for both the relative constancy and the slow change of the race made up as it is of such mortal units as individuals More specifically, we must study the make up of the individual and learn how replacements are made when individuals wear out

THE CELLULAR MAKE UP OF INDIVIDUALS

All living things, except possibly the filterable viruses and bacteriophages are made up of vital units known as *cells* Many of the

lower organisms are unicellular, but all of the higher organisms are multicellular

A complex organism such as a man or an insect consists of millions of cells Each cell bears a life of its own, but is dependent for its supplies of food and oxygen upon other cells, and in turn performs some function that is of value to the organism as a whole The division of labor and interdependence of the innumerable cells of the cell republic, the organism, is reflected in the fact that groups of cells of a particular sort constitute tissues, that various combinations of tissues form organs, and that various combinations of organs form systems, such as the nervous system, the digestive system, the circulatory system, and others No matter how elaborate the specialization of organs and systems may be, every living part is composed of cells Cells are perhaps the most fundamental units of life in about the same sense that atoms are the fundamental units of matter itself Also, cells possess certain mechanisms which are the principal agents both in preserving constancy of form and function (heredity) and in promoting diversity and change (variation) Hence if we desire to understand how evolution takes place, it behooves us to make a careful examination of the constitution of cells

A TYPICAL CELL AND ITS COMPONENT PARTS

Cells vary in size and in form according to the special functions they subserve, but in spite of their numerous specializations they have many features in common The diagram of a cell shown in Figure 40 is not meant to represent any particular kind of cell, but is a composite of many kinds of cells Of course no one kind of cell contains all of the cell organs shown in this diagram

The two most important subdivisions of the cell are the nucleus and the cytosome or cytoplasm

The nucleus is a more or less centrally situated body commonly spherical in form, and separated most of the time from the cytosome by a *nuclear membrane* Within the nucleus is a characteristic material known as *chromatin*, which at times condenses into definite bodies known as *chromosomes* each chromosome consisting of a bundle of *genes*, or hereditary units

The cytosome consists of all the rest of the cell except the nucleus All the vast hordes of cells of different sorts constituting a given complex organism are identical in their nuclei, but in any cell the cytoplasm differs in its form and structure according to its location in the

organism and its special function Thus a nerve cell and a muscle cell of a given organism may be utterly different in general form and function, but the nuclei of both are the same Since the specific hereditary materials of the individual are possessed equally by all of the cells of that individual it follows that the differences in cells and tissues must be solely cytoplasmic How these differences arise is a problem

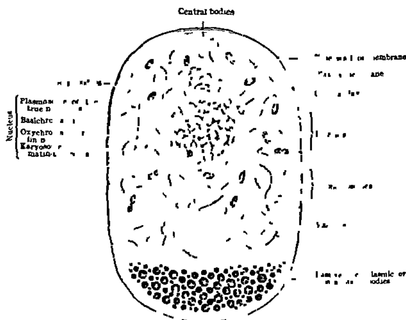


FIG 40 —Diagram of a typical cell Its cytoplasmic basis is shown as a granular meshwork or framework in which are suspended various differentiated granules fabrillae and other formed components (*From E B Wilson*)

of individual development rather than one of racial evolution Many of the slow and steady trends in evolution, however, are believed by some authorities to be the result of general hereditary changes in the cytoplasm, but there is a great deal of evidence favoring the conclusion that the nucleus is the chief organ of heredity and of variation in the cell

Details of the nucleus —The nucleus except during the process of mitotic cell division is surrounded by a definite membrane, the *nuclear membrane,* which separates the clear *nuclear sap* from the cytoplasm outside the nucleus During the resting stage, between two cell divisions, there is a network of *linin* fibers running throughout the nucleus

Upon this linin network are strung numerous granules of a deeply staining substance, or substances, called *chromatin granules* Other nuclear bodies, known as *nucleoli*, *plasmosomes*, and *karyosomes*, are found in some nuclei, but they may be ignored so far as our knowledge of their rôle in evolution is concerned

Chromosomes —Far more important for our purposes than any other cellular components are the *chromosomes* Preparatory to the process of mitosis the diffusely scattered granules of chromatin condense into semi solid masses, sometimes spherical or ovoid, sometimes rodlike, sometimes V shaped, etc These are the chromosomes Each species of organism possesses in all its cells a certain definite number and kind of chromosomes Man has 48, *Drosophila melanogaster* has 8, *Oenothera lamarckiana* has 14, *Ascaris megalocephala* has 4 in one variety and 2 in another, some crustaceans and some roses have over a hundred chromosomes Careful studies of the chromosomes of numerous species of both animals and plants have revealed the significant fact that, except in the males of some species, the numbers of chromosomes are *even* Furthermore, it is possible to match them up in pairs according to their sizes and shapes The significance of this becomes clear when we remember the fact that an individual starts out from a *zygote* (fertilized egg) which is a composite cell to which each parent has contributed one full set of chromosomes

Genes —At this time it seems well to anticipate the later results of genetic research to the extent of stating that each kind of chromosome contains a unique series of hereditary units (genes) Certain genes lie in certain chromosomes, and all the genes in a particular chromosome are probably arranged in linear order like beads on a string Since the orderly arrangement of genes in bundles (chromosomes) and their specific arrangement within a given bundle are both important in heredity, it is essential that this specific organization be maintained during development and reproduction It is also essential for persistence of type from generation to generation that the complete organization, not only of nucleus but of the cytosome, be maintained This is accomplished by that heredity mechanism par excellence, the *mechanism of mitosis*

The central body.—Imbedded in the cytoplasm, usually in close proximity to the nuclear membrane, lies a structure known as the *central body* (*centrosome*) In most animal cells this structure is well defined, but it is absent in most plant cells The central body is primarily associated with cell division, as will be seen later

CELL DIVISION—MITOSIS

Each cell during periods of growth and development grows to a definite size and then divides into two daughter cells Repeated cell divisions multiply vastly the numbers of cells in a developing embryo, until in higher organisms millions of cells are produced To make what might easily be a long story as short as possible, let it be sufficient to state that the chief features of mitotic cell division (mitosis) are as follows The central body divides, and the two centers migrate apart, spinning between them a spindle of fibers, the *mitotic spindle* (Fig 41) The nuclear membrane disappears, and, as the two central bodies migrate farther and farther apart the chromosomes, which have in the meantime gradually become more and more compact, move toward the equator of the spindle, each attached by two fibers probably composed of linin, one fiber leading to one pole of the spindle, the other fiber to the other pole (Fig 42) Usually even before migrating into the spindle each chromosome has become a double body, a pair of joined twins, each one the exact duplicate from end to end of the other Each gene in the gene chain has previously twinned, so that each gene in each chromosome is a double or twin gene The chromosomes now arrange themselves in a plane at right angles to the long axis of the spindle, each chromosome having one of its twin halves directed to one pole and the other to the opposite pole All of the stages up to this point of equilibrium are known as *prophases* of mitosis, the equilibrium phase being the *metaphase* (Fig 42, *E*)

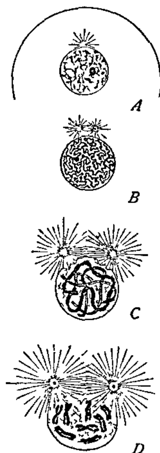
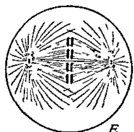
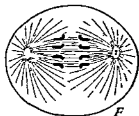


FIG 41 —Diagram of the early phases of mitosis in *Ascaris* *A* vegetative nucleus *B* fine spireme *C* coarse spireme *D* late prophase with chromosomes spindles forming (*From E B Wilson*)

Now the real separation phase of division begins The twin components of each chromosome seem to be pulled apart, possibly by the fibers attached to them, and one twin migrates to one pole, the other twin to the other (Fig 43, *H*) Slowly the various chromosome twins approach opposite poles and finally cluster closely about the latter At this point the cell wall constricts at the equator and soon divides the single cell into twin daughter cells (Fig 43, *I*) Not only are the chromosomes divided meticulously into equal lots, but all the cytoplasmic parts of the cell are so divided that each daughter cell comes to have exactly the same detailed organization as had the mother cell from which they were derived The period during which chromosome halves migrate to the poles of the spindle is called the *anaphase*, while that during which the chromosomes lose their density and reform the chromatin network with which we started is called the *telophase*





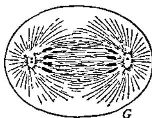


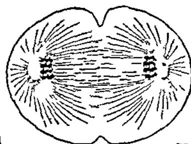
Fig 4 —Diagram of the middle phases of mitosis *E* metaphase *F* *G* earlier and later anaphases (*From Wilson*)

By means of this elaborate routine of division the exact specific organization of the cell is maintained at least in the *germ track* In this process of mitosis we have a view of the mechanics of heredity, which, if uninterrupted, would maintain perfect constancy of type for all time unless a new order of environment were to alter the expression of a fixed hereditary complex, or some other mechanism promoting diversity were to intervene

DIFFERENTIATION

Not merely do cells multiply in the process of embryonic development, but at every step differentiation of cells for the performance of different specialized functions is going on The mechanism of differentiation is at present very incompletely understood and what we do know is of a technical nature and difficult to present without a back

ground of embryological lore In very brief it must suffice for present purposes to state that differentiation is accomplished partially by unequal cell division in which the two daughter cells come to possess different cytoplasmic contents partially by the differences in position of cells with respect to the environment partially by differences in the relations of certain cells to other cells that have already assumed special characters owing to their original position or their special relation to the environment and partially by the fact that certain genes are effective only at a given time in development or when cells are in a certain physiological state All cells in an organism are believed to possess the same genes but particular genes become effective only under special conditions of time and place Some such complex of intricate interrelations at present very obscure even to the most advanced students of embryology seems to underly cellular differentiation While the geneticist cannot avoid all responsibility for the solution of these insistent problems he may with some appropriateness delegate them for the present at least to the experimental embryologist At any rate it seems best at the present juncture to sidestep the problems of differentiation and to get back on surer ground more familiar to geneticists and more applicable to their problems



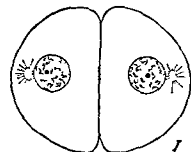


FIG 43 —Diagram of the end phases of mitosis *H* the beginning of constriction of the cell membrane *I* the completed division (*From Wilson*)

THE ORIGIN OF NEW INDIVIDUALS

MODES OF REPRODUCTION

Since individuals the temporary components of the race or species are continually running their courses and dying off replacements are necessary if the race is to persist The replacement of old individuals by new is commonly called *reproduction* There are numerous modes

of reproduction, but they may all be classified into two main categories *somatogenic* and *cytogenic* Somatogenic reproduction is accomplished without the instrumentality of sex and involves the subdivision of the parent body into two or many fragments each of which has the power to reconstitute a whole new individual like the parent In unicellular organisms somatogenic reproduction involves the division of the one celled body into two or more cells each capable of growing into a full sized individual in multicellular organisms the products of division are multicellular fragments Cytogenic reproduction is accomplished by means of unicellular germ cells which must pass through processes of growth and division in order to reconstitute the multicellular body typical of the species to which they belong

The essential feature of all reproductive processes is that some portion of the parent is isolated or physically cut off from the parent s body an integral part of which it formerly was On ceasing to be a part of an organized system it exercises its prerogative of developing a system of its own in the image of the one from which it was derived This is true whether the isolated part be a single cell or a multicellular fragment This is perhaps to be expected in view of the fact that each cell possesses the hereditary organization characteristic of the race or species

Varieties of somatogenic reproduction —In *unicellular organisms* the principal modes of sexless reproduction are transverse fission in which the division is across the long axis of the cell longitudinal fission in which the division is parallel with the long axis and multiple fission in which the nucleus divides several times before the cytoplasm partitions the several nuclei off to form separate cells In *multicellular organisms* the principle modes of somatogenic reproduction correspond rather closely to those among unicellulars but several special modes are added *Transverse fission* is common among worms of various kinds and among the larvae of certain jelly fishes *Longitudinal fission* takes place in the early embryos of a number of mammals as in armadillos and in man resulting in true quadruplets and true twins derived from an original single embryo *Multiple fission* occurs in a number of parasitic insects in which the multicellular embryo subdivides into hundreds of cell masses each of which becomes a complete individual In addition to these types of fission multicellular organisms reproduce by *budding* which may be simple or multiple Budding involves the outgrowth of a minor portion of the parent body, the latter body being left intact—this being in contrast with

fission processes in which the entire parent body is distributed among the progeny *Gemmulation* is a peculiar form of somatogenic repro duction found among sponges involving the gathering together of samples of all the various kinds of cells into compact little balls called *gemmules*, which survive the dead parent and escape to form new sponges when the parent body disintegtrates

Artificial propagation of both plants and animals is made possible through the ability of many organisms to regenerate a whole new in dividual from a small part of a parent organism Thus sponges may be cut up into minute fragments and distributed like seeds upon a slab of concrete, each fragment growing up into a sponge of the parental type Everyone is familiar with the fact that gardeners propagate many plants by planting cuttings and that potato tubers (enlarged parts of the underground stem) may be cut into as many fragments as there are "eyes and that each will produce a plant with tubers like the parental tuber

All the cells involved in somatogenic reproduction are the product of ordinary mitotic division which maintains so painstakingly the hereditary organization of the species No wonder, then, that this mode of reproduction makes for a high degree of constancy of type Apart from the effects of differences in the environment, which appear not to be inherited there is nothing about somatogenic reproduction to favor diversity or change If one desires to study pure heredity uncomplicated by sex and its diversifying effects, one should study successive generations produced by somatogenic reproduction

Varieties of cytogenic reproduction —All those forms of reproduc tion in which single cells become separated from parent bodies to give rise to new individuals fall into this category The first and simplest form of cytogenic reproduction is *spore formation* Among plants, reproduction by spores is well nigh universal, though many also make use of gametes A spore is nothing more than a small cell produced by mitosis from previous cells Spores are commonly motile, some being furnished with flagella by means of which they travel through the water, others being so light as to be wind borne To reproduce a new organism, a spore, after a period of rest, merely divides and redivides and thus forms a new multicellular body

In some of the lower plants motile spores, all visibly similar, swim about actively in swarms, and then pair off two by two and fuse to form *zygotes* from which new plants develop These mating cells are called *gametes* This is the most primitive expression of sex in plants

Further specialization of sex cells involves, first, the differentiation of gametes into large passive gametes (*eggs*) and small motile gametes (*sperms*) and, second, the differentiation of sex individuals, *males* and *females*

At this point, it is important to emphasize the fact that sex, although it appears to be so intimately associated with reproduction, is in no way essential to reproduction In fact, it is a hindrance rather than a help to the mere multiplication of individuals Sex is a mechanism that has been superimposed upon reproduction and has a function only remotely associated with the latter In a word, sex is the *diversity mechanism*, with which we shall deal fully at the proper time

The *female gamete, or egg,* is always relatively large Even the tiniest of eggs, such as those of placental mammals, are relatively large as compared with tissue cells The human egg (ovum), for example, has a cubic content of about a thousand times that of the average tissue cell, *while the eggs of birds and sharks are thousands of times bulkier* than mammalian eggs This great increase in the size of eggs is due largely to the accumulation of food material (yolk) that serves to sustain the embryo and give it a good start in life Most eggs are, when *full grown, spherical or ovoid in form, and most of them are protected* by envelopes of one kind or another

Male gametes, or *sperms*, are highly variable in shape and are relatively extremely small and active Most of the cytoplasm of the sperm is specialized for locomotor purposes Some sperms have one long tail like a snake (Fig 47 *f*), others have two or several tails, and still others have numerous radiating locomotor processes resembling the thorns of a sand burr In general, a sperm gives the impression of being a highly specialized cell one of whose main functions is that of finding and penetrating the egg Sperms are thousands, sometimes millions, of times as numerous as eggs, thus making it more probable that at least one sperm will reach each mature egg

When the sperm approaches the egg it seems to be guided at least in some cases, by a specific chemical substance given off by the egg When egg and sperm meet, the latter penetrates the former more or less completely (Fig 50, *a*) Sometimes the whole sperm enters the egg sometimes only the head of the sperm containing the nucleus and a minute amount of cytoplasm On entering the egg cytoplasm, the sperm nucleus grows at the expense of the latter and becomes nearly or quite as large as the egg nucleus (Fig 50, *c*, *d*, *e*) The union of egg and sperm is called *fertilization*, and the product of the union is a *zygote*

The term "zygote' is also sometimes used to designate the organism that develops from the united gametes

Gametic reproduction is very frequently evaded in both animals and plants by the use of a process known as *parthenogenesis*, or "virgin birth," in which eggs develop without any aid from sperms Some instances of this peculiar aberration of gametic reproduction will be discussed in a special chapter on the biology of sex (chap xvii) Here we have the anomalous situation of gametic (or marrying) reproduction without the presence of both sexes Long-continued parthogenesis involves the reduction of diversity and results in constancy as marked as that which is associated with various forms of sexless reproduction

While the great majority of animals and plants are sexually dimorphic consisting of male individuals that produce sperms and female individuals that produce eggs, large numbers of both animals and plants are *monoecious*, having both sexes present in one individual Such forms among animals are known as *hermaphrodites* In some hermaphrodites eggs are fertilized by own sperms, in others mating occurs in which a mutual exchange of sperms takes place In the latter instances the advantages of sex in enhancing diversity are retained, and mating is facilitated because any two adult individuals may mate, but in the former instances where self fertilization occurs, diversity is reduced to the level found among organisms reproducing by asexual methods It is possible, therefore, to produce from such self fertilizing monoecious species *pure lines* in which all progeny of a single individual are genetically identical In a later connection we shall make use of such forms as these to study heredity in its simplest expression (chap xv)

THE ORIGIN OF GAMETES

Two important questions arise in connection with gametes (*a*) From what cells in the parent body do gametes arise? (*b*) What changes occur in germ cells that make it possible for them to unite in pairs to form zygotes?

The germ track —The question as to whether germ cells are derived from parental tissues that have been more or less specialized for other functions, or whether they are derived from an unbroken series of germ cells set apart from bodily functioning at all times, is one of great importance for theories of heredity The prevailing view of biologists is that, at least in the higher animals, and possibly in all animals and plants, the germ cells are produced from cells that have never in any

generation gone through a period of specialization for any particular bodily function In animals these cells are believed to be set apart early in ontogeny (the development of the individual) and localized in *sex glands*, or *gonads* In plants the germ track is believed to be maintained in the meristematic cells of growing points but germ cells are not so definitely localized as in most animals

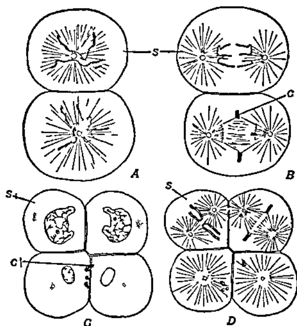


FIG 44 —The germ track in *Ascaris* Stages in early cleavage showing the chromatin diminution process in all cells except the stem cell (*S*) (*From Boveri 1897*)

In some animals the germ track is very clear and unmistakable from the beginning of one generation to that of the next The classic instances of germinal continuity are those of the roundworm, *Ascaris megalocephala*, and the fly, *Miastor americana*

In the variety of *Ascaris* known as *univalens*, which possesses only two chromosomes to each cell (incidentally the lowest number known), the developmental stages are as follows at the first division of the zygote two cells are formed in the usual way, each cell with two long loop-like chromosomes (Fig 44 *A*) One of these two cells, however, undergoes a striking nuclear change involving the breaking off of the

ends of the chromosomes and the disintegration into small chromatin granules of the middle portions The large ends of the chromosomes are discarded into the cytoplasm and absorbed, while the smaller granules are all that the descendants of this cell have for chromosomes It is significant that the progeny of such cells form only body cells, in this case skin and nerve cells (Fig 44, *A*) The other cell remains just like the original zygote and is a stem cell or germ cell This cell then divides, and one of the daughter cells retains the full germinal character, while the other breaks down its chromosomes as before and gives rise to tissues that line the digestive tract (Fig 44, *B*) Once more the germ cell divides and one of its daughter cells undergoes chromosome breakdown, its cell progeny forming chiefly such tissues as muscles, blood vessels, and connective tissues (Fig 44, *D*) From this point on, the germ cells are definitely set apart and contribute no further to the soma They give rise to nothing but germ cells and ultimately to gametes The unbroken series of cells with intact chromosomes from the zygote to gametes is the *germ track*, and the chromosomes of these cells carry the so called *germ plasm* The rest of the embryo constitutes the *soma* or *somatoplasm* The relation of body to germ plasm is well shown in the accompanying diagram (Fig 45)

A second example of a well defined germ track is found in *Miastor* (Fig 46 *A*) in which a single definite germ cell (*p g c*) is set aside at the very first division of the zygote The other cell divides repeatedly, casting out parts of the chromosomes, as in *Ascaris*, and ultimately giving rise to all the soma Even in a fairly advanced embryo (Fig 46 *B*) the large germ cells are clearly seen in a small group (*oog*) These give rise ultimately to the gametes

While in vertebrates the germ track is ill defined and difficult to follow, there seems to be no doubt that it exists Some investigators, however, claim that the original primordial germ cells disintegrate and come to naught and that the gametes arise from a new lot of germ cells that are derived afresh from generalized epithelium If that be the case it seems fair to consider this epithelium as part of the germ track and not as a differentiated part of the soma At least it may be said with confidence that in none of the higher mammals are germ cells ever derived from specialized body cells such as muscle cells, nerve cells, or gland cells Our question as to the origin of the germ cells seems to be answered They are derived in an unbroken series from previous germ cells by the process of mitosis This is the basis of Weismann's concept of *the continuity of the germ plasm*

THE MATURING OF GAMETES

The primordial germ cells, previously described as having been set apart from the soma at a relatively early period of development and located in germ glands (*ovaries* and *testes*), pass through a period of comparative inactivity until sexual maturity arrives At the dawn

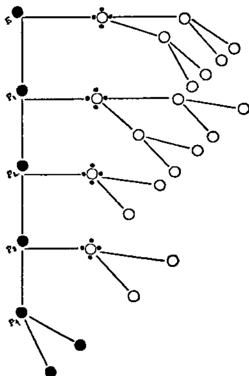


FIG 45 —Diagram of the germ track in *Ascaris* *E* egg P_1 P_2 P_3 stem (germinal) cells P_4 primordial germ cell Circles represent somatic cells while the four black dots outside of the circles represent the masses of chromatin that are eliminated (*From Boveri 1910*)

of sexual maturity the germ cells wake up and enter upon a period of great activity, during which mature gametes are produced The history of the production of gametes differs somewhat in the two sexes That of the male, called *spermatogenesis*, is a little simpler than that of the female, called *oogenesis*, and will be described first

Spermatogenesis —The first sign of renewed activity of the male germ cells is evidenced by a succession of rapid cell divisions, the

mechanism of mitosis being used After many thousands of germ cells have been produced, multiplication is stopped and growth sets in, the growth in the male cells being very slight as compared with that of female cells During the period of growth the chromosomes not only split to form twin chromosomes, as though in preparation for mitosis, but whole homologous chromosomes unite in pairs, a process known

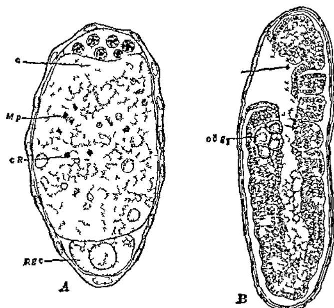


FIG 46 —The germ track in *Miastor americana* *A* germ-cell (*p g c*) set apart in the eight-celled stage of cleavage (*After Hegner*) The walls of the remaining

as *synapsis* The result is that instead of the set of single chromosomes characteristic of the zygote there are groups of four (*tetrads*) each tetrad composed of two pairs of twin chromosomes bound together There are just half as many tetrads as there are chromosomes in the zygote Now follow two special cell divisions, known as *meiosis*, without any further change in the chromosomes The result is that one chromosome of each tetrad goes to each of the four matured sperm cells In one of these divisions, the so-called *reduction division*, both twins of an originally single chromosome pass together to one cell,

which results in a reduction of the number of chromosomes characteristic of the zygote to one half (Fig 47) The other division simply separates twin chromosomes as in ordinary mitosis The result is that each gamete has only one of each kind of chromosome and therefore only one half the number possessed by the zygote and the primordial germ cells It is customary to speak of the somatic or zygotic

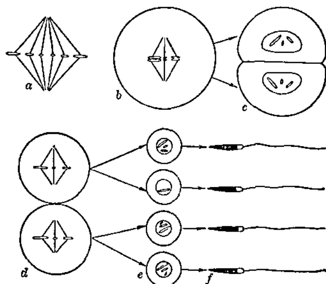


FIG 47 —Diagram to illustrate spermatogenesis *a* showing the diploid number of chromosomes (six is arbitrarily chosen) as they occur in divisions of ordinary cells and spermatogonia *b* the pairing (synapsis) of corresponding mates in the primary spermatocyte preparatory to reduction *c* each secondary spermatocyte receives three the haploid number of chromosomes *d* division of the secondary spermatocytes to form *e* spermatids which transform into *f* spermatozoa (*From Guyer*)

number as *diploid* or *2n* and the gametic number as *haploid*, or *n* The final phase of spermatogenesis consists of an elaborate specialization of the male gamete, consisting of the development of locomotor organs and adaptations for penetrating the egg

Oögenesis —The period of multiplication is essentially the same as in *spermatogenesis except that fewer and larger cells are produced* The period of growth is very marked for it is during this period that the egg accumulates the yolk which is usually massed at the vegetal pole The nucleus and central body confined to a small region of

clear protoplasm at the animal pole, are not in a position to bring about an equal cell division Hence the maturation divisions are very unequal (Fig 48) The first maturation division results in a large cell not appreciably smaller than the full grown egg and a very tiny cell called the *first polar body* The second maturation division results in a *second polar body* and the mature female gamete, or unfertilized egg Sometimes the first polar body divides again, sometimes not Typically, however, four female gametes are produced, corresponding in

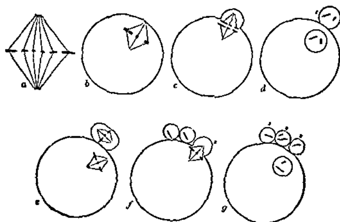


Fig 48 —Diagram to illustrate oogenesis *a* showing the diploid number of chromosomes (six is arbitrarily chosen) as they occur in ordinary cells and in oogonia *b* the pairing of corresponding mates preparatory to reduction *c d* the [illegible] the reduced or haploid number of chromosomes (*From Guyer*)

number to male gametes similarly produced, but three out of every four eggs, namely, the polar bodies, are abortive and die because of deficiency of cytoplasm, leaving only the one large well nourished egg as the progeny of each primordial germ cell that completed the period of growth Synapsis and the reduction division are the same in oogenesis as in spermatogenesis (Fig 49)

Now, during both spermatogenesis and oogenesis the united pairs of homologous chromosomes, one derived from the father and one from the mother of the previous generation, arrange themselves during the reduction division quite independently of one another, so that some maternal and some paternal chromosomes enter each gamete Where

there are large numbers of chromosomes, very many different assortments of maternal and paternal chromosomes are produced This shuffling and dealing of parental heredity materials constitutes one of the principal means of increasing diversity in organisms and therefore one of the most important mechanisms of evolution A relatively

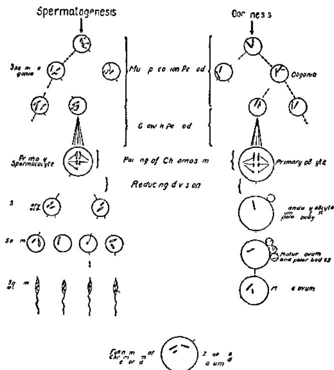


FIG 49 Diagram showing the parallel between maturation of the sperm cell and maturation of the ovum (*From Guyer*)

simple case of the assortment of different chromosomes to gametes is shown in Figure 99

THE UNION OF GAMETES—FERTILIZATION

Once the gametes are mature they are ready for the fertilization process (Fig 50) It seems to be a matter of pure chance that any particular sperm finds and enters any particular egg Since there are usually hundreds of different kinds of eggs and equally large numbers of different kinds of sperms the number of possible kinds of zygotes produced is extremely great If, for example a species has only

twenty chromosomes—less than half that possessed by man—there would be $(2)^{10}$, or 1,024 different gametes in each sex And since each kind of egg is as likely to be fertilized by one kind of sperm as another, there might be produced $(1024)^2$, or 1,048,576 different zygotes Hence, meiosis and fertilization together constitute an extremely effec-

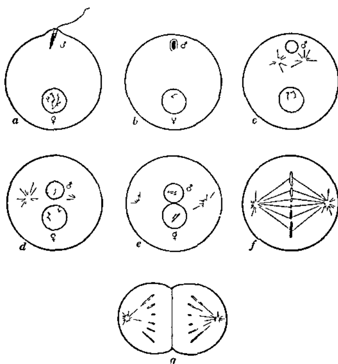


Fig 50 —Diagram to illustrate fertilization ♂, male pronucleus ♀, female pronucleus observe that the chromosomes of maternal and paternal origin respectively do not fuse (*From Guyer*)

tive mechanism for increasing diversity This is the chief rôle played by sex in evolution

This abbreviated account of biological processes is all that is needed for our purpose and should, we believe, enable the student to follow intelligently the accounts of heredity, variation, selection and isolation that are to follow A more detailed account of the processes of mitosis, meiosis, and fertilization may be found in chapter xliv, "The Mechanism of Mendelian Heredity"

CHAPTER XV

INTRODUCTION TO THE STUDY OF PERSISTENCE FACTORS

As was pointed out in chapter xiii, the principal agents that make for constancy or persistence of type from generation to generation are (*a*), the relative stability of the units of heredity genes, (*b*) the relative stability of the bundles of genes, chromosomes (*c*), the relative precision and perfection in operation of mitosis, (*d*) the relative constancy of the environment over long periods

Laborious studies of gene changes, especially in the fruit fly, *Drosophila*, have shown that genes are exceedingly stable Muller and Altenberg have discovered that a large proportion of the genes of *Drosophila* must have a stability comparable with that of the atoms of the element radium, which have an average unchanged life of about two thousand years Of course, where there are hundreds, possibly thousands, of genes in each cell, the chances of some gene change being observed during any given period will depend upon the numbers of genes present and the number of individuals examined

Chromosomes are probably almost equally stable except for crossing over, a phenomenon that cannot be discussed here Changes in numbers and composition of chromosomes do occur as rare accidents of mitosis or meiosis, and these changes break up the constancy of cellular organization, but the relative constancy of chromosomal numbers and of their genic content constitutes one of the most important agents in maintaining persistence of types

Various kinds of irregularities in the characteristically constant and nearly perfect mechanism of mitosis are responsible for rare changes in chromosome numbers and for redistribution of genes in chromosomes, but these events are so rare that they only very slightly affect the constancy of the species of animals and plants in which they occur

Another factor influencing persistence that is likely to be neglected is that of the relative constancy of the environment in any given geographic region It is well known that, apart from seasonal fluctuations, the general climatic conditions in a given region remain unchanged over long periods of time The mean annual temperature,

the mean annual rainfall and the general character and direction of air movements remain essentially the same for very long periods Such constancy of environment could hardly fail to exercise a standardizing effect upon animal and plant communities and thus aid in maintaining constancy in the expression of racial characters

Persistence and diversity mechanisms contrasted —It is customary in courses in genetics to introduce the study of heredity by presenting an outline of Mendelian heredity This seems to us a mistake, for Mendelian heredity is really not essentially a persistence factor but rather a most effective diversity factor It breaks up constancy of combinations of unit characters and promotes multiplicity of recombinations of such characters For this reason we shall begin our discussion of the persistence factors in evolution with the study of heredity in *pure lines* in which the persistence mechanism is free to operate without being complicated by the diversity mechanism Since biometric methods are necessary for the study of variation and heredity in pure lines it is necessary to introduce a brief statement about these methods

A short lesson in biometry —When character differences are either qualitative or are sharply defined they are easily handled by Mendelian methods If for example all individuals are either black or white tall or short heavy or light and no gradations occur between the two alternatives it is easy to follow the distinct types through successive generations If on the other hand there occur all gradations between black and white all gradations between tall and short and all gradations between heavy and light it is no longer possible to classify each individual in some particular category When this is the case the only possible method of finding out how much is inherited and how much is not is to study whole generations of progeny as units and to determine what is the characteristic of one whole generation as compared with the next whole generation Such a comparison requires statistical methods

Suppose for example we want to find out whether the size of bean seeds is hereditary or merely environmental we shall have to measure the seeds of the parent and compare them with those of the offspring There would be nothing gained by comparing a selected seed of the parent with one of the offspring We must compare the total of one with the total of the other It is necessary then to find a method or methods of comparing the parent condition as a whole with the offspring condition as a whole Some simple method must be devised

that gives due credit to each of the variants in the two generations One method commonly used is the graphic method Thus each seed of the parent generation is measured and plotted on a graph in which the horizontal line (the abscissa) represents a series of size classes varying from the smallest ones at one end and the largest at the other, and the perpendicular line (the ordinate) represents the frequencies of individuals in the varying size classes A line connecting high points in each of the size classes will form a *variation curve* which will be characteristic of the group Such a curve has a high point near the middle (called the *mode*), and the curve slopes gradually toward each end This curve not only represents the distribution of the different sizes in the group but shows the most commonly occurring size class the modal class A similar curve is made for the offspring generation, and the parent curve is compared with the offspring curve The two may be compared with respect to mode, mean, average, and standard deviation, and a great deal may be learned, that can be learned in no other way, about the variation and heredity of such graduated or fluctuating characters as weight

For further information about statistical methods in genetics, the reader is referred to a short chapter in the Appendix (chap xliii) It will hardly be necessary here to do more than indicate that pure-line work, such as that of Johannsen, Jennings, Tower, and Wright discussed in the next chapter, could not have been done without the use of biometrical methods

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The first thing he did was to collect all the seeds (we would call them beans) from a single bean plant, which is a male female individu al These beans were of many different sizes, some quite large, others quite small, and many intermediate In order to follow the heredity of bean size with accuracy, he weighed each bean on a delicate balance What he determined was the weight of each bean, but we shall speak of large and small size instead of heavy and light weight Since some few of the beans were very large and some few very small, what more natural than to select the largest beans to be the seeds for the next generation of plants, and to expect that the beans of the next and the next and the next generation would be larger and larger and larger?

If Johannsen was sanguine enough to expect to get such a rapid improvement in beans he was doomed to disappointment He had constructed a curve of variation, in the manner described in the last chapter, for beans of the parent plant This curve had a definite shape and a definite mode When he constructed a similar variation curve for the progeny derived from the largest beans of the first gener ation this curve was practically the same as that of the parent genera tion The beans were not all large, as he may have hoped but some were large, some small and many intermediate just as in the parent generation Continuing to select, for planting the largest beans for six generations he found that there had been no change in the average size of beans, and the number of largest beans had not increased Selection then had been powerless when operating upon individuals with identical heredity

Another series of breeding experiments was carried out, selecting for seed the smallest beans of the original parent plant of Pure Line I The bean progeny of the second generation differed not at all from those derived from the largest bean of this pure line They gave the same variation curve and the same average as the latter, and this was maintained for six generations It made no difference whether the largest the smallest, or the average beans were selected for planting so long as they belonged to the same pure line the same variation curve and the same average were maintained

A second pure line, which we may call Pure Line II, was started from another parent plant, chosen because the average size of beans was distinctly less than that of the first pure line The statistical study of the beans of this second parent plant revealed another new and significant fact, namely, that the beans, when arranged accord ing to sizes, gave a variation curve differing markedly from that of

Pure Line I The shape of the curve the mode, and average size were different. Again selection for six generations of first, the largest beans for seed, and second the smallest beans for seed, did not affect the variation curve mode or average Once again, selection within a pure line was quite ineffective

The same results were obtained in all the rest of the nineteen orig inal pure lines with which Johannsen experimented

A somewhat more concrete idea of the results obtained may be secured through the perusal of the following table which gives in terms

RESULTS OF SELECTION IN PURE LINE I

Harvest Year	Mean Weight of Selected Parent Seed		Mean Weight of Offspring	
	Minus	Plus	From Minus Parent	From Plus Parent
1902	60	70	63 15	64 83
1903	55	80	75 19	70 88
1904	50	87	54 59	56 68
1905	43	73	63 55	63 64
1906	46	84	74 38	73 00
1907	56	81	69 07	67 66

of average bean weight the results of selecting plus and minus parents for six generations in Pure Line I the plus parents being largest beans and minus parents being smallest beans

It will be seen that in the last year of this selection experiment (1907) the smallest beans averaging 56 cg in weight, produced a prog eny weighing, on the average 69 07 cg , while the largest beans of the same year, averaging 81 cg , produced progeny of practically the same average weight as did the smallest beans namely, 67 66 cg The dif ference is not statistically significant The influence of the environ ment in bean weight is clearly shown in the data for the year 1904 which was a bad year for growth In this year, the average weight of progeny from both large and small beans was greatly reduced, being respectively 56 68 cg and 54 59 cg That this loss in weight was not inherited is shown by the results in subsequent years in which the average returned to that seen in the first year of selection It is also interesting to note that in the years 1903 1906 and 1907 the lighter parents produced a heavier progeny than did the heavier parents

From these experiments Johannsen came to the conclusion that plus and minus fluctuations about the mode were due to differences in

the environment and were not inherited, and that what was really inherited was merely a potentiality to produce beans of a certain average weight which may be modified by the environment It was also obvious that these environmental modifications had no effect on subsequent generations, that is to say, they are not inherited Selection therefore, has no effect unless there are hereditary differences among the individuals selected

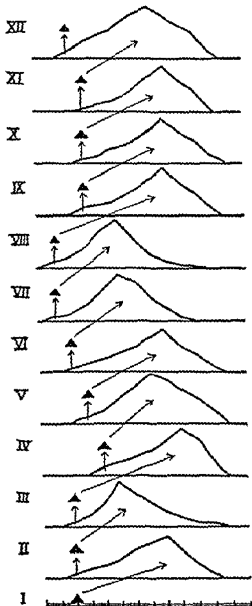
All the members of a given pure line are identical genetically that is there are no differences in their genes Johannsen called a group of individuals that are alike in their genes a *genotype*, and spoke of all such individuals, whether alike in seed size or not, as *genotypically* identical Hence individuals that breed alike, whether they look alike or not, are members of the same genotype On the other hand, each of the nineteen pure lines is a different genotype though some beans in each pure line may be exactly of the same size as some beans in others Johannsen designated individuals that look alike and have the same somatic characteristics whether they are genotypically alike or not members of the same *phenotype*, in other words, they may be *phenotypically* identical though *genotypically* different Phenotypic differences, unless also associated with genotypic differences are not hereditary This conclusion is a highly important one for all our further study of heredity

Another significant conclusion may be reached from these experiments namely that environmentally produced differences if they are merely phenotypic in character play no important part in evolution, except in so far as they may favor the survival of certain individuals possessing genotypic differences Hence environmentally produced differences in the soma have only an indirect influence on the course of evolution

OTHER EXAMPLES OF PURE LINES

W L Tower in a long series of experiments on the potato beetle, *Leptinotarsa decemlineata* came to similar conclusions He produced a pure line not by making use of a self fertilizing species, but by closely inbreeding a bisexual family for a long time This stock was tested and found to be genotypically pure, yet there was a considerable amount of variability in the shade of color in the color patterns and in other ways For twelve generations he selected and bred from the darkest specimens and from the lightest specimens, keeping the two series separate (Fig 51) The result was that instead of getting

darker specimens predominating in one series and lighter specimens in the other, he obtained a final generation of individuals showing practically the same range of variability in both series, and in neither series was there any consistent change from the condition present at the beginning of the experiment



More recently *Sewall Wright*, working in connection with the Bureau of Animal Industry, has produced a considerable number of pure lines by long continued brother and sister mating in guinea pigs Sixteen families have been established by over thirty generations of the closest possible inbreeding No selection was practiced The result was that most of the pure lines showed marked reduction in fertility and in vigor, as compared with the control cross bred stock Each line, however, differed from all the others in these

FIG 51 —Diagram to illustrate the results of selection in pure lines Ineffectiveness of selection through twelve generations within a homozygous strain in the case of the Colorado potato-beetle (*Leph notarsa*) In each generation extreme dark specimens were selected as the parents of the succeeding generation but the progeny always swung back to the type (*After Tower*)

respects, as well as in many others Members of any pure lines were remarkably uniform but there was also a fair amount of fluctuation with respect to quantitative characters Even such characters as the shape and extent of color markings, weight, fertility, etc , showed considerable individual variability, but none of these differences proved to be hereditary

Jennings tried still another type of pure line material using organisms *that reproduce by binary fission* He worked with a number of differing clones (pure lines produced asexually) of Paramecium, a common ciliate protozoan Each selected Paramecium was isolated in a separate culture vessel, where it was allowed to multiply for several generations Size differences and other measurable differences were noted in the original isolated parent individuals, and those of all the progeny were measured, plotted, and averaged It was found that a different mean, mode, and average size was characteristic for each pure line If the largest individual is then isolated from each culture and bred for a number of generations, its progeny will be of the same average proportions as that of the stock from which the largest individual had been chosen, for they are genotypically unchanged though differing phenotypically

Exactly what is inherited?—All that is passed on from one generation to another is an organized mass of protoplasm, or in gametic reproduction two such organized masses—an egg and a sperm that unite to form a zygote Characters, as such, are not transmitted or passed on A zygote, the biologic heritage, has no eyes, no feet no brain, no instincts All it possesses is a very definite nuclear and cytoplasmic organization, which, under an appropriate environment, has the potentiality of producing a new individual with characters whose expression may be more or less modified by the differences in the environment within the organism or outside of it

Specifically, let us state exactly what was inherited in Johannsen's pure lines Pure Line I differs in its hereditary potentialities from Pure Line II in that, under the given conditions of the environment, it produces on the average heavier beans than Pure Line II is able to produce If a particular bean chosen from Pure Line I and one from Pure Line II were allowed to develop under exactly the same environment, the offspring of Pure Line I would be heavier than that of Pure Line II But if the environment of Pure Line II were better than that of Pure Line I, it might readily produce larger beans that the latter But this environmentally induced difference would not be inherited

Exactly what then is inherited? A certain complex of genes and a certain cytoplasmic organization are all that can be said to be inherited These heritages are to be conceived of as potentialities capable of working with the environment to produce individuals with certain particular characters Individuals will differ from one another partly because the materials constituting the zygote are different and partly because their environments are different To what extent heredity and environment determine individual differences we must not attempt to decide at present We shall be in a much better position to deal with this problem after we have discussed the other factors of the evolution mechanism

CHAPTER XVII

SEX DETERMINATION AND SEX DIFFERENTIATION

Introductory statement —In chapter xiv we have spoken of sexual reproduction as one of the modes of cytogenic reproduction We have also referred several times to the ways in which sexual reproduction constitutes the main mechanism of diversity Two questions with regard to sex, however, have not yet been broached (*a*) What determines the sex of the individual? (*b*) How do the secondary sexual characters of individuals develop? These two questions will be answered in the present chapter

SEX DETERMINATION

The question as to what determines whether an animal shall be a male or a female is a very ancient one, and it is only during the present century that we have solved the puzzle

A great many theories of sex determination have been proposed, some of which are as follows

a) Hippocrates and some subsequent theorists believed that the sex of the offspring depended on the relative vigor of the parents, the more vigorous parent giving his or her sex to the offspring

b) Thury thought that the sex of the offspring depended on the degree of ripeness of the ovum at the time of fertilization

c) Various writers claim that statistics show that germ cells from *the right ovary produce males and those from the left ovary females*

d) *The nutrition theory* —The egg is a much more highly nourished cell than the spermatozoon, and the idea seems natural that high degrees of nourishment of the mother produce female offspring and lower degrees of nourishment male offspring Professor Schenk of Vienna gained a huge reputation by controlling the diet of certain royal prospective mothers and predicting the sex of the offspring accordingly He was correct in his predictions several times, but his success was short lived His early predictions were merely lucky, just as one might be who could guess heads or tails correctly several times in succession

Some color is lent to the nutrition hypothesis by the fact, if it is a fact, that after war or famine, when the nutrition of mothers has been

low more males than females are born. This is probably a case of differential prenatal mortality. By that we mean that more females die unborn than males because the latter are hardier and stand prenatal malnutrition better.

e) *Sex is determined at the time of fertilization.*—Perhaps the best evidence that sex is determined at the very beginning of development

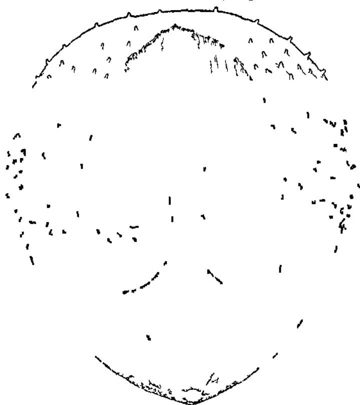


Fig. 52.—An armadillo egg about six weeks after fertilization showing the quadruplet fetuses derived from the single egg, and all destined to be of the same sex. (*From Newman.*)

is derived from one egg twins and quadruplets. In the nine banded armadillo practically every female gives birth to quadruplets, four essentially identical young being produced in each litter. All in a given set of quadruplets are invariably of the same sex, either four males or four females. Newman and Patterson have shown that each set of quadruplets comes from a single egg, which at a very early stage

divides into four parts to form four fetuses (Fig 52) The conclusion is that sex was determined before the separation took place Human identical twins, also always of the same sex in a pair, furnish further evidence in favor of very early sex determination These and numerous other similar facts justify the conclusion that sex is determined at the time of fertilization

THE CHROMOSOMAL MECHANISM OF SEX DETERMINATION

In two previous chapters (chaps xv and xvi) descriptions of the typical modes of chromosomal sex determination have been given In order to facilitate a clear understanding of this important matter it seems well to recapitulate one typical instance Perhaps the best known instance of sex determination is that of *Drosophila melanogaster* already described and figured (Fig 53) by Babcock and Clausen In this insect the female body cells and the unmaturated germ cells are characterized by the presence of two sex chromosomes (X-chromosomes), which are shown in black at the top of the left hand column of the accompanying figure The chromosomes are readily distinguishable by being of medium size and straight The male body cells and unmaturated germ cells (top of right column) are just like those of the female except that there is substituted for one of the X-chromosomes a hook-like chromosome, known as a Y chromosome. Now in the process of maturation of the germ cells, which results in the formation of gametes with the haploid or half somatic number of chromosomes, each of the eggs (female gametes) receives an X chromosome All eggs are therefore alike in their chromosome content, including the sex chromosome The case is different on the male side for two kinds of gametes are formed, one kind with an X-chromosome and the other with a Y chromosome These are formed in exactly equal numbers, as one of each is produced at every reduction division Each egg must be fertilized by one or the other of these two kinds of sperms, and in the long run as many eggs will receive an X-chromosome as will receive a Y chromosome Those that receive an X-chromosome will be characterized by having two X-chromosomes, which is the typical female condition, and thus a new female individual is started in life, while those that receive no X chromosome, but a Y-chromosome, will have the XY composition characteristic of the male sex, and will give rise to males The female sex may thus be designated as XX and the male sex as XY We have shown for *Drosophila* the exact mechanism that operates in determining whether an individual

shall be a male or a female, and in addition we have explained why equal numbers of both sexes are continuously produced

How general is the chromosomal mechanism of sex-determina-

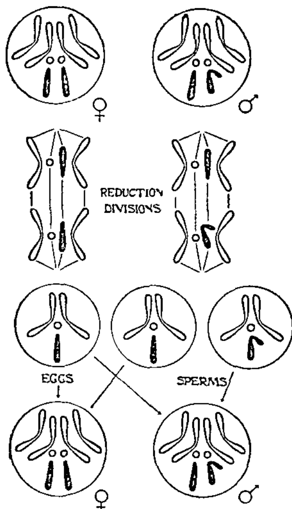


FIG 53 —Diagram showing chromosome relations in the determination of sex in *Drosophila ampelophila* (*From Babcock and Clausen*)

tion?—"To what extent," says E B Wilson, "sex may be determined by an automatically operating nuclear mechanism such as has been here described is unknown, but a mechanism that exists in the same

general form in organisms as diverse as bryophytes, nematodes, echinoderms, arthropods and vertebrates is beyond a doubt of far reaching significance, and may be as widely distributed as Mendelian heredity generally While the same general scheme holds for all forms that have been investigated, there exist many interesting differences in the details of operation of the sex-determining machine Some of the simpler variations of the process are as follows

a) Variations of the Y-chromosome —Beginning with a condition such as that described for *Drosophila* in which the Y chromosome is larger than the X chromosome, there is a long series of species in which the Y chromosome becomes smaller and smaller until it dwindles away to nothing and the male chromosome condition becomes XO instead of XY In the females of such species the condition remains XX

b) Variations of the X chromosome —In a number of species of animals the X-chromosome may be represented by from two to nine components, each of which at times has the appearance of a separate chromosome In a species of roundworms, *Ascaris canis*, for example the diploid chromosome number of the female is thirty six and that of the male is thirty, the difference being due to the fact that there are two sets of six X components in the female and only one set in the male In the reduction division of the male germ cell the six X components all go in a group to one gamete and none to the other so that two kinds of gametes are produced, one with eighteen chromosomes and the other with twelve chromosomes All the female gametes have eighteen chromosomes Apart from the fact that the X chromosome is in six pieces instead of but one the mechanism of sex determination is the same as it is in a group that has but one X chromosome

c) Linkage of sex chromosome with autosome —In a great many species of insects the X chromosome has been found to be united to one end of one of the autosomes, never losing this relation during the entire chromosome cycle Apart from this apparently secondary union with an autosome, the behavior of the X chromosome is the same as in the XO cases described above Hence the mode of sex determination is in line with the types already discussed

d) Female digamety —In this mode of sex determination two different kinds of eggs are produced, while the sperms are all alike In other words, there is simply an exchange between the sexes of the nuclear differences characterizing males and females Thus in the Lepidoptera (butterflies and moths) the females have either the XY or the XO type of chromosome complex while the males always have the XX condi

tion Though the cytological evidence is still incomplete, it is practically certain that birds have the same peculiar method of chromosomal sex determination as the Lepidoptera, for they have the same type of sex linked heredity as the latter and the opposite of that seen in mammals and most insects Apart from the change of the digametic condition from one sex to the other, the mechanism remains the same

Sex chromosomes in parthenogenesis —When it became known that parthenogenetic species (those in which eggs are capable of developing without fertilization) in some cases produce males and in other cases produce females from parthenogenetic eggs, this seemed to be out of accord with the theory of the chromosome mechanism of sex determination It is interesting to know, however, that, now that we know the histories of the chromosome cycles in these species, the facts are not only fully in accord with the chromosome theory, but greatly strengthen it and enlarge its range of applicability Two kinds of parthenogenesis are known, which may be designated *diploid* and *haploid* In the former, the developing egg and embryo has the full somatic number of chromosomes in the latter, only half the somatic number characteristic of the species is present

a) *Diploid parthenogenesis* —In these species only one maturation division occurs and this division is not the reduction division, hence each egg retains the diploid number of chromosomes, including two X-chromosomes (XX) The result is that all eggs that behave in this way develop into females Thus in aphids and phyloxerans many successive generations of all females are produced After a series of female generations a mixed generation appears in which males are produced parthenogenetically along with females, but from smaller eggs Examination reveals the fact that male-producing eggs have after maturation two less chromosomes than the female-producing eggs This was explained by the observation that when the first maturation takes place, two chromosomes (obviously consisting of a double X element) are cast out into the polar body, while all the autosomes and two of the X chromosomes remain in the egg nucleus In this way the male produced from this egg comes to have only two X-chromosomes, while the female has four This is really the equivalent of XX for the female and XO for the male In gamete formation the males produce two kinds of gametes, one with the double X-element and the other with no X element Only the former of these is viable, and this accounts for the fact that all fertilized eggs produce females, for both gametes supply double X-elements. This

whole rather intricate story is thus seen to be merely a variant upon the typical scheme of chromosomal sex determination

b) Haploid parthenogenesis —This kind of parthenogenesis is now known to occur in rotifers, in several orders of insects, and in arachnids It is practically universal among the Hymenoptera (bees, wasps ants, etc.), and we may use the case of the honey bee as an illustration In haploid parthenogenesis the egg develops after having undergone the reduction division it therefore has only half the somatic number of chromosomes, including but one X chromosome Invariably the progeny from haploid parthenogenesis are males which we might expect from the fact that they have but one X-chromosome In the bees the queen seems to be able to determine whether an egg gets fertilized or not An egg descends the oviduct, passes the seminal receptacle containing a supply of sperms acquired during the mating act and if sperms are given off, fertilization occurs and a female is produced, but if an egg slips past the seminal receptacle without being fertilized, the result is a male (drone) Now these drones are the mates of the future queens and must supply the spermatozoa for the next generation of eggs They already possess the reduced number of chromosomes so they cannot well undergo the reduction division in forming gametes It is interesting to note, however, that a sort of vestigial reduction division takes place resulting in the formation of a tiny cell without any nucleus and a larger cell with all the chromosomes (including one X-chromosome) characteristic of males of the species A second maturation division divides chromosomes lengthwise Since all gametes both male and female contain an X chromosome fertilization always results in a female Thus once more the general sex determination formula is confirmed

Sex chromosomes in hermaphrodites and gynandromorphs —*Hermaphrodites* are individuals which are functionally both male and female that produce both eggs and sperms in the same body Hermaphroditism is common in snails flatworms, earthworms nematodes tunicates and in several other phyla of animals We have unfortunately very little information about the chromosome situations in these forms In one species of nematode (*Angiostomum nigrovenosum*) however, it is known that there is an alternation of generations between a parasitic hermaphroditic generation and a free living dioecious generation (with separate males and females) In the dioecious generation males and females are about equally numerous All fertilized eggs of this generation produce parasitic hermaphrodites These produce from their gonads first oogonia and later spermatogonia the form

er producing eggs and the latter spermatozoa It is known that all eggs of the hermaphrodite generation have six chromosomes, while the sperms have either five or six Self fertilization takes place, and half of the fertilized eggs produce males with (eleven chromosomes) and half produce females (with twelve chromosomes) of the free-living generation The males of the dioecious generation produce two kinds of gametes with respectively five and six chromosomes, and one would expect males and females to be produced from fertilization, but this is not what happens for only hermaphrodite individuals with twelve chromosomes are produced It seems certain that only one of the two kinds of spermatozoa (that with six chromosomes) is viable, and that the hermaphrodite generation is chromosomally female How can a female produce spermatozoa of two kinds, one with six and the other with five chromosomes? This is explained by the fact that in the second maturation division one of the X-chromosomes remains near the equator of the spindle, and does not become included within the daughter nucleus Thus one of the daughter cells is without an X chromosome and is male-producing when fertilization takes place Further investigation of the chromosomes of hermaphrodites will doubtless be in agreement with what we already know

Gynandromorphs are individuals made up of some female body regions and some male body regions Thus, an insect may have male secondary sexual characters on one half of the body and female characters on the other, or the anterior end may be male and the posterior, female The chromosomal basis for these conditions is not entirely clear, but Morgan and Bridges have shown that all of the peculiarities of the hereditary behavior can be explained on the assumption that in the first or second cleavage division one of the X chromosomes lags behind and is excluded from one of the daughter cells Thus one daughter cell gets XX and the other X, which accounts for the fact that all the cell descendants of one cell have the female characters and all those of the other cell, male characters

Intersexes and their bearing on sex determination —Bridges, during his experiments with *Drosophila*, encountered in certain strains anomalous individuals that were neither male nor female, but *intersexes* On cytological examination these were found to have a changed chromosome complex One type, for example, was found to have three of one kind of autosomes (instead of the usual two) but only two X-chromosomes The interesexual condition in this case might be explained by the assumption that the autosomes have a male-produc

ing tendency and that one set of extra autosomes is sufficient partially to overcome the female tendency of two X-chromosomes, thus producing intersexes Again individuals with three X-chromosomes but only the usual supply of autosomes were super females somatically but unbalanced in their physiology and non viable These results show that in the words of E B Wilson, '*the actual performance of the zygote, therefore, is the common effect of the whole group, and is turned this way or that as the result of a quantitative balance between X-chromosomes and autosomes*'

SEX DIFFERENTIATION

It now becomes necessary to distinguish clearly between sex determination and sex differentiation When we say that by means of a chromosomal mechanism sex is determined, exactly what do we mean? We answer that the sex of an individual arising from a fertilized egg (in the case of parthenogenesis, an unfertilized egg) has been settled. Now as a matter of fact only one thing has been settled irrevocably, and that is that one individual will have the chromosome composition characteristic of a male and another individual that of a female A male is usually an individual that produces spermatozoa and a female one that produces ova Is it irrevocably settled beyond possibility of reversal that a zygote with the XX chromosome composition must produce eggs and one with the X composition, spermatozoa? This question has apparently been answered by Geoffrey Smith in his work on parasitically castrated crabs and by Richard Goldschmidt on Gypsy moths In the first case, individual crabs whose testes had been infested by the parasitic cirripede *Sacculina*, were gradually changed over in their whole metabolism to such an extent that cells destined to produce spermatozoa produced ova In the second case, when certain varieties of moth were crossed, all of the germ cells produced females with ova whereas half of the eggs had the XX and half the X chromosome content This evidently means that some individuals with the male chromosome character produced eggs From these results we may be justified in concluding that not even this most fundamental difference of sexes that of the female producing ova and the male spermatozoa is irrevocably predetermined at fertilization

Lest the reader be confused, however, we hasten to add that under natural conditions of life an individual with the male chromosomal content produces spermatozoa and one with the female chromosomal content produces eggs, and that only rare accidental or unnatural

conditions disturb the normal course of events For purposes of practical genetics we may then define a female as an individual that produces ova and a male as one that produces spermatozoa

Secondary sexual characters—Usually males and females differ from each other in many other characters besides the production of eggs or sperm Often one sex is larger, stronger, more elaborately ornamented and colored than the other and possesses characteristic accessory sex organs whose function it is to facilitate the bringing together of the eggs and the sperm All of the differences between the sexes other than the primary difference of egg or sperm production are called *secondary sexual characters* Usually very young animals show only slight differences in secondary sexual characters and the differences increase markedly at sexual maturity We speak of the gradual divergent development of the two sex types as sex differentiation The question arises as to whether or not the chromosomal differences are the causes of the differentiation of secondary sexual characters These secondary sexual characters are all somatic, and, since the soma is the product of cell division of the zygote, the soma cells must have either the male or the female chromosomal character That the chromosomal mechanism in the somatic cells is not sufficient of itself to bring about, unaided the differentiation of secondary sexual characters can be shown readily in at least many animals

In the mammals, for example, it is known that the early removal of the testes or ovaries results in a retention of the juvenile or undifferentiated condition of secondary sexual characters Evidently some influence is exerted by the tissues of the gonad that is necessary for the full differentiation of sex characters The current theory is that certain glandular cells that form part of the body of ovary or testes excrete materials into the blood that stimulate various tissues in different ways and produce dimorphic results The specific substances produced by these glands are called "hormones,' for want of a better name To test the efficiency of these hormones the crucial experiment of taking out the gonads of a young rat or guinea pig and implanting the gonad of an individual of the opposite sex has been many times performed For example, Steinach castrated young male rats and then successfully grafted into them ovaries from young female rats The result was that these young rats which started to be males became much altered in a female direction, the mammary glands becoming greatly enlarged their instincts more feminine than masculine, and in a number of other particulars they showed more or less pronounced evidences of feminization Conversely, spayed

females with engrafted testes showed a tendency toward male differentiation, especially in instincts These experiments have been largely confirmed by C R Moore

In birds it is of interest to note that practically complete reversal of secondary sexual characters may be induced if young females are entirely deprived of the ovary The condition is described by L V Domm as follows

"The larger percentage of our birds have assumed additional male characters following removal of the ovaries, until they are practically complete replicas of the male, and, to those not familiar with their history, they are regarded as unmistakable males Thus we find that they assume the complete male plumage, spurs grow as they do in the normal cock, head furnishings increase in size until they can not be distinguished from those of the normal male

"Other birds in the pen regard them as males and when a strange cock is introduced they fight as would other cocks, very frequently assuming the initiative, some of them having been observed to come off victorious *in such a combat Many of these birds crow regularly* When aroused by a disturbance, it was found that their reaction is very similar to that of the male, the sounds they make, together with their reaction on such occasions, reminds one very much of the young male just prior to maturity

"*One set of experiments may be mentioned as an example* Out of the one lot of fourteen females of the same hatch, one was kept as control and thirteen were operated upon between the ages of six weeks and six months, twelve of these have developed all the characteristics of the male mentioned above some being completely cock feathered, *while the others are fast becoming so The other one of the thirteen* is very capon like in appearance except perhaps for size and can not be readily distinguished from her capon brothers by those not knowing her history This bird has assumed complete male plumage is developing spurs but the comb, wattles and earlobes are pale and small, *resembling those of the capon*

"In some of our cases individuals which have assumed more or less complete male characters as concerns head furnishings, plumage and spurs, are reverting toward the female type as shown by the female type of plumage reappearing

"*Our results indicate that the female in the brown leghorn fowl* has many potentialities of the male, which are normally inhibited by the presence of the ovary, and that these potentialities can assert

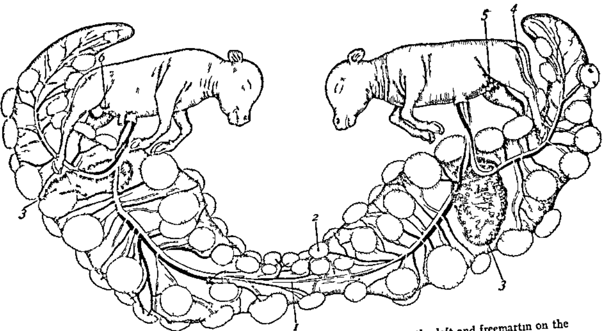


Fig 54 —A typical opposite sexed pair of cattle twins male on the left and freemartin on the right showing (1) the connecting artery between the two twins (2) a single placental cotyledon entered by veins from both foetuses (3) opening cut into the chorion through which the foetuses have been removed (4) clitoris of the freemartin, (5) the well-separated anterior and posterior teats characteristic of the male (6) the much closer teats characteristic of the female (*From Newman after Lillie*)

themselves approximately fully after the complete removal of the ovary at an early age"

A beautiful experiment conducted by nature herself helps to drive home the *hormone theory of sex differentiation* In cattle as shown recently by F R Lillie, twins occur in a small percentage of cases and involve the simultaneous fertilization of two eggs These eggs lie as a rule in opposite horns of the forked uterus, but owing to the growth of their embryonic membranes the two individuals come to fuse circulations so that there is an admixture of blood (Fig 54) The result is that if the twins are zygotically of the same sex no untoward effect of blood admixture is apparent, but when the twins are zygotically a male and a female the female individual is always stopped in its female differentiation and becomes more or less completely transformed in a male direction It appears however that at the time when blood admixture occurs, the female individual has already differentiated so far with respect to the external genitalia and in other respects that, even though subsequent development be entirely male in character, the resultant individual is always a sterile creature, neither fully a female nor a complete male Such individuals have long been known as 'freemartins" As a rare exception to the general rule an occasional case has appeared in which a male and a female pair fail to undergo blood admixture In such cases both develop into normal animals It now appears that the reason why the female sex is the one to suffer is that the male gonads differentiate precociously, before the female, and inhibit the subsequent development of female gonads Hence the only hormones in the blood of both twins are the male hormones

In conclusion we may say then that in mammals, though chromosomes tend to determine the primary sex differences, they have no effect on the differentiation of secondary sexual characters These are due to substances secreted by the gonads that have been called hormones

CHAPTER XVIII

MENDEL'S LAWS OF HEREDITY

MENDEL S LIFE AND CHARACTER[1]

J ARTHUR THOMSON

Gregor Johann Mendel was born in 1822, the son of well to-do peasants in Austrian Silesia He became a priest in 1847, and studied physics and natural science at Vienna from 1851 to 1853 Thence he returned to his cloister and became a teacher in the Realschule at Brunn It was his hobby to make hybridisation experiments with peas and other plants in the garden of the monastery, of which he eventually became abbot Apart from two papers, one dealing with peas and a shorter one with hawkweeds, and some meteorological observations, he does not seem to have published much But what he did publish, if small in quantity, was large in quality He died in 1884

MENDEL'S DISCOVERIES

In 1866 Gregor Johann Mendel, Abbot of Brünn, published what some regard as one of the greatest of biological discoveries After many years of patient experimenting chiefly with the edible pea, he reached a very important conclusion in regard to the inbreeding of hybrids, which is often briefly referred to as "Mendel's Law" His publication was practically buried in the Proceedings of the Natural History Society of Brunn, those who knew of it, as Nageli for instance did, failed to realise its importance in fact, Mendel's epoch making work was lost sight of amid the enthusiasm and controversy which the promulgation of Darwinism (1858) had evoked. Mendel's Law seems to have been rediscovered independently in 1900 by the botanists De Vries, Correns, and Tschermak, and to Mr Bateson we owe much, not only for his recognition of the far reaching importance of the abbot's work, but also for a notable series of experiments in which he has confirmed and extended it

[1] From J Arthur Thomson *Heredity* (copyright 1907) Used by special permission of the publishers, John Murray, London.

Mendel's experiments —What Mendel sought to discover was the law of inheritance in hybrid varieties and he selected for experiment the edible pea (*Pisum sativum*) The trial plants, he says, must possess constant differentiating characters, and must admit of easy artificial pollination, the hybrids of the plants must be readily fertile, and readily protectable from the influence of foreign pollen These conditions were afforded by peas, and twenty two varieties or subspecies of pea were selected, which remained constant during the eight years of the experiments Whether they were called species, or sub species, or varieties, is a matter of convenience, the names *Pisum quadratum*, *P saccharatum*, *P umbellatum*, etc , do in any case represent groups of similar individuals which breed true *inter se* It should be noted that these peas have the particular advantage, for experimental purposes, that they are habitually self fertilised—in North Europe, at least

In studying the different forms of peas, Mendel found that there were seven differentiating characters which could be relied on

1 The form of the ripe seeds, whether roundish, with shallow wrinkles or none, or angular and deeply wrinkled

2 The colour of the reserve material in the cotyledons—pale yellow, bright yellow, orange, or green,

3 The colour of the seed coats, whether white, as in most peas with white flowers, or grey, grey brown, leather brown, with or with out violet spots, and so on,

4 The form of the ripe pods, whether simply inflated, or con stricted, or wrinkled,

5 The colour of the unripe pods, whether light or dark green, or vividly yellow, this colour being correlated with that of stalk, leaf veins, and blossoms,

6 The position of the flowers, whether axial or terminal, and

7 The length of the stem, whether tall or dwarfish

Mendel's results, the Law of Dominance —Having defined the differentiating characteristics of the varieties, Mendel proceeded to make crosses between these, investigating one character at a time Thus, pollen from a pea of the round seeded variety was transferred to the stigma of a pea of the angular seeded variety, the stamens of the artificially pollinated flower being, of course removed before they were ripe The same was done all along the line

What was the result in the hybrid or cross-bred offspring? It was found that they showed one of each pair of contrasted characters to

the total, or almost total, exclusion of the other No intermediate forms appeared

Mendel called the character that prevailed dominant, and the character that was suppressed, or apparently suppressed, recessive And the first big result was that crosses between a plant with the dominant character and a plant with the recessive character yielded offspring all resembling the dominant parent as regards the character in question Let us for shortness call the parents D and R, and the first result may be expressed thus $D \times R = D$

It must be carefully noted that the *complete* dominance which Mendel observed has been shown in other cases to be the exception rather than the rule Thus a cross between a "Chinese" primula with wavy crenated petals and a "star" primula with flat simply notched petals is intermediate between the two parents, and yet, as the next generation shows, the case is one of Mendelian inheritance

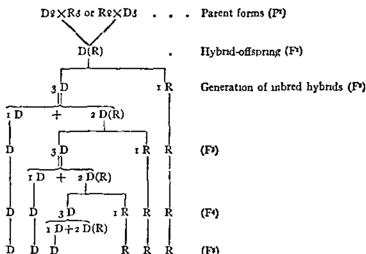
In many cases the hybrid, while on the whole dominant, may show some influence of the recessive character but not nearly enough to warrant us in speaking of a blend Thus, when white (dominant) Leghorn poultry are crossed with brown (recessive) Leghorn, most of the offspring have some "ticks" of colour When these are inbred they produce a quarter brown (extracted recessives) and three-quarters pure white or white with a few ticks The dominance is not quite perfect

The Law of Splitting or Segregation.—In the next generation the cross-bred plants (products of D and R, or R and D, but all apparently like D) were allowed to fertilise themselves, with the result that their offspring exhibited *the two original forms*, on the average three dominants to one recessive Out of 1 064 plants, 787 were tall, 277 were dwarfs

When these recessive dwarfs were allowed to fertilise themselves they gave rise to recessives only, for any number of generations The recessive character bred true

When the dominants, on the other hand, were allowed to fertilise themselves, one-third of them produced "pure" dominants, which in subsequent generations gave rise to dominants only, and two-thirds of them produced once again the characteristic mixture of dominants and recessives in the proportion of 3 1

The general results may be expressed in the scheme The result of the hybridisation is a generation (F_1) like the dominant parent They may be represented by the symbol D(R), for they



carry with them the possibility of having offspring with the recessive character, that is to say, the recessive character remains latent in the inheritance

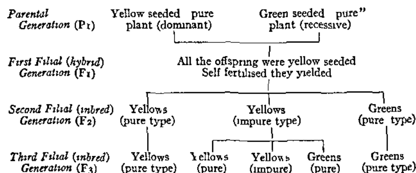
When these D(R)s are inbred (self fertilised, in the case of peas) they have offspring (F_2), some of which resemble the recessive parent, while others resemble the dominant parent, and these occur in the proportion of 1 3 When those resembling the recessive parent are inbred, they breed true—i e , they give rise to a line of pure recessives Those resembling the dominant parent are all apparently alike, but their subsequent history shows that they may be divided into a set which breed true to the dominant type and a set which behave like the first generation of hybrids—i e , they go on splitting up into dominant like forms and pure recessives These two sets occur in the proportions of 1 2

A case of peas —Let us consider a concrete case Peas with rounded seeds were crossed with peas having angular wrinkled seeds In the offspring the character of roundness was dominant, the angular wrinkled character had disappeared or receded It was not *lost*, as the next generation showed

The hybrid offspring all with rounded seeds, were allowed to self fertilise In their progeny roundish seeds and angular wrinkled seeds occurred in the proportions of 3 1 Here were the recessives again, and when *they* were allowed to self fertilise they produced pure recessives only, with angular wrinkled seeds

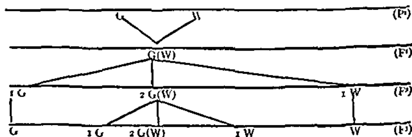
The dominants, however, were not all pure dominants, for when they were allowed to self fertilise they produced one-third pure dominants and two thirds ' impure ' dominants, the latter being distinguished by the fact that in their offspring recessives reappeared in the proportion of one recessive to three dominants

The outstanding facts, taking the case of yellow seeded and green seeded peas may be thus summarised —



Thus intercrossing of forms with contrasted characters results not in transitional blends, but in the dominance of one character and the recession of another Self fertilisation (the extreme of inbreeding) of the hybrids results in a number of pure recessives and a number of dominants in the proportion 1 3 some of these dominants (one-third) are pure, and produce only dominants some (two-thirds) are apparently pure, but produce dominants and recessives in the old proportion, 3 1

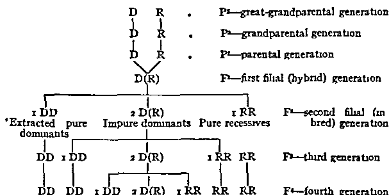
A case of mice —*Let us take a concrete case from among animals* A grey house-mouse is crossed with a white mouse, the offspring are all grey Greyness is dominant albinism is recessive



The grey hybrids are inbred, their offspring are grey and white in the proportion 3 1 If these whites are inbred they show themselves "pure," for they produce whites only for subsequent generations But when the greys are inbred they show themselves of two kinds, for one-third of them produce only greys, which go on producing greys, while the other two-thirds, apparently the same produce both greys and whites And so it goes on.

Summary —In his exceedingly clear exposition of Mendelism (1905) Mr R C Punnett states the result thus ' Wherever there occurs a pair of differentiating characters of which one is dominant to the other, three possibilities exist there are recessives which always breed true to the recessive character, there are dominants which breed true to the dominant character, and are therefore pure, and thirdly, there are dominants which may be called impure, and which on self fertilisation (or in breeding, where the sexes are separate) give both dominant and recessive forms in the fixed proportion of three of the former to one of the latter "

Schematic representation of Mendel's Law —Following Mr Punnett's suggestion, with slight modifications, we may use the symbols P_1, P_2, P_3 for the parental, grandparental, and great grandparental generations, F_1 for the first filial (hybrid) generations, F_2, F_3 F_4 for the subsequent inbred generations The symbol D(R) means a dominant with the recessive character unexpressed, but potentially present, DD or RR means pure "extracted ' dominants or recessives—i e, those pure forms which are sifted out from the inbreeding of "impure" dominants



MENDEL S EXPLANATIONS[1]

JOHN M COULTER AND MERLE C COULTER

Mendel s explanation of this behavior involved three theses which at that time were new to biology These theses must be kept distinct from one another

1 **Independent unit characters** —This means that an organism although representing a morphological and physiological unity, from the standpoint of heredity is a complex of a large number of independent heritable units Thus if one pea plant is tall and another one is dwarf the behavior of the hybrid produced from them with reference to this character will be the same, no matter what other characters the parent plants may have had In other words, the characters are *independent units*, unaffected by other characters or units The character of tallness from a tall plant with wrinkled seeds or purple flowers will act just the same as from a tall plant with smooth seeds or white flowers Tallness is a unit and its behavior in inheritance is independent of all other units

2 **Dominance** —In the germ plasm there are certain determiners of unit characters which dominate during the development of the body, causing these characters to dominate over others and thus become visible The characters dominated over and thus not allowed to express themselves are called *recessive* characters. These recessive characters are present in the germ plasm, but cannot express themselves and become visible as long as the *dominant* characters are present. When a dominant character is absent, however, its recessive alternate is free to express itself and become visible

For example in the case of tall and dwarf peas tallness is a dominant character and dwarfness is its alternative recessive When a dwarf appears therefore, there is present no dominant tallness to suppress it In the F_1 generation all the individuals were tall because although they had all received the recessive character of dwarfness from one of the parents they had received the dominant character of tallness from the other parent, and so dwarfness did not appear in any of them Such pairs of alternative characters are now commonly called *allelomorphs* Thus tallness and dwarfness are allelomorphs in the pea one dominant over the other which is therefore recessive

3 **Purity of gametes** —A gamete can contain only one of two alternative characters For example, it may contain the character

[1] From Coulter and Coulter *Plant Genetics* (The University of Chicago Press copyright 1918)

for tallness or for dwarfness, but not both In other words, allelo morphs cannot be represented in the same gamete If the gamete having the character for tallness unites with one having the character for dwarfness, the resulting zygote will contain both, but will produce a tall individual because tallness is dominant over dwarfness When this tall hybrid produces gametes, however, one-half of them will contain the character for dwarfness Thus the alternative characters are "segregated" in gamete formation and no gamete will have both characters

These three theses, independent unit characters, dominance, and purity of gametes (better called segregation), make up the theoretical explanation of Mendel's law Independent unit characters was of course a necessary conception It was original with Mendel, and has also been original with other investigators, but this conception does not represent the essential feature of Mendel's law The idea of dominance had been somewhat vaguely proposed before Mendel's time In the old literature on animal breeding one meets theories of prepotency, which were proposed again and again before the discovery of Mendel's work in 1900 In any event Mendel was the first to formulate definitely the theory of dominance among unit characters It should be realized also that dominance is not an essential feature of Mendel's theory Many cases are known in which dominance fails but in other regards the Mendelian inheritance is strictly followed

The essential feature of Mendel's theory is his conception of the *purity of gametes*, brought about by the segregation of alternative characters The striking fact is that this conception, purely theoretical with Mendel, has since been confirmed by cytology In the mechanism of cell division each chromosome is divided into two equal parts and each daughter cell receives one of these parts It is a reasonable inference that chromosomes are bearers of hereditary characters In the production of gametes the number of chromosomes, characteristic of the organism is reduced one half As a consequence each gamete carries only one half the characters of the individual that produced it An application of these statements to an explanation of Mendel's 3 1 ratio will illustrate the situation

For convenience we will assume that the nuclei of Mendel's peas have four chromosomes each (Fig 55) In the case of a tall plant two of the four chromosomes carry the character for tallness that is, something that determines the production of the tall character in the somatoplasm, which is practically the *body builder* This unknown

something is called by various names in the literature of genetics, the commonest one being *determiner* In our illustration, therefore two of the four chromosomes carry the determiner for tallness At this point two questions may be asked

1 Why do just two of the four chromosomes carry the determiner for tallness rather than all of them or only one of them? Just here it would be difficult to explain why no more than two of the four chromosomes are represented as carrying the same determiner This will be explained later It is easy to answer, however, why the determiner is being carried by more than one chromosome When gametes are formed the chromosome number is reduced one half Since every gamete from a pure tall plant carries the determiner for tallness there

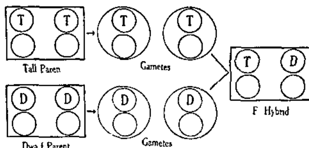


Fig 55.—Diagram illustrating behavior of chromosomes in Mendel s cross of tall and dwarf peas Large rectangular figures nuclei of zygotes or mature individuals large circles gametes small circles within zygotes and gametes chromosomes letters on chromosomes determiners (*T* tallness *D*, dwarfness) (*From Coulter and Coulter*)

must have been at least two chromosomes carrying the determiner before the gametes were formed

2 Do these two chromosomes carry any other determiner than that for tallness? In a tentative way this question may be answered in the affirmative but a fuller discussion of the situation must be deferred There is much experimental evidence that indicates that more than one determiner is carried on a single chromosome In some cases also there are more Mendelian determiners than there are chromosomes

The situation is represented in Figure 55 This shows a somatic cell with the diploid or $2x$ number of chromosomes In the formation of gametes this number is reduced to the haploid, or x number, which in this case is two The diagram shows that the reduction separates

(segregates) the two chromosomes carrying the character for tallness so that each gamete contains one This occurs for the other characters as well as for that of tallness From the tall plant, therefore all the gametes will contain the character for tallness and from a dwarf plant all of the gametes would contain the character for dwarfness When these two individuals are crossed the zygote will contain both charac ters and these two characters will be transmitted together in the succeeding cell generations The individual from such a zygote of course would be tall but at the same time it would be carrying a recessive determiner for dwarfness and this fact would be shown by

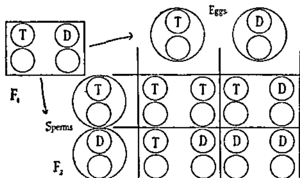


FIG 56 —Diagram illustrating behavior of first hybrid generation (F) when inbred Illustrates meaning of segregation and purity of gametes and how chance matings of F_1 gametes result in 3 1 ratio in F generation dwarf individual produced only by zygote in lower right hand corner (*From Coulter and Coulter*)

its behavior in breeding The result of inbreeding such hybrids is indicated in the accompanying diagram (Fig 56) which represents the chance matings of two kinds of gametes The obvious results are three tall individuals and one dwarf This is the so-called *monohybrid ratio* which means the ratio when a single pair of allelomorphs is considered

Before discussing the further development of Mendel s law it will be necessary to explain some of the terminology of genetics When each gamete carries the same kind of determiner the zygote is said to receive a *double dose* when a zygote receives only a single such deter miner it is said to receive a *single dose* In Figure 56 one zygote receives a double dose of tallness and two others a single dose These phrases are more or less common in the literature of the subject but the more

frequent terminology is as follows When two similar gametes unite to form a zygote it is called a *homozygote*, when the two pairing gametes are different the zygote is called a *heterozygote* Using this terminology it is evident that the 3 1 ratio of the F_2 generation is really a 1 2 1 ratio as follows 1 homozygote for the dominant character, 2 heterozygotes and 1 homozygote for the recessive character The 1 2 1 ratio therefore is the significant one and appears as a 3 1 ratio only because of dominance

In the experiment represented in Figure 56 three tall individuals appear in the F_2 generation Superficially the individuals look alike but it is realized that 1 differs from the other 2 in germinal constitution, for 1 will produce only one kind of gamete while the other 2 will produce two kinds To indicate this situation Johannsen has introduced some appropriate terminology Organisms which seem to be alike, regardless of their germinal constitution, are said to be *phenotypically* alike or to belong to the same *phenotype* On the other hand organisms having identical germinal constitution are said to be *genotypically* alike or to belong to the same *genotype* From the standpoint of phenotypes only, Mendel s F_2 generation shows the 3 1 ratio but if genotypes are considered it shows the 1 2 1 ratio In other words this group of forms contains two phenotypes but three genotypes

Referring again to Figure 56 several things may be inferred It can be seen what will happen in the F_3 generation when the F_2 individuals are inbred The dominant homozygote will produce only dominant homozygotes in the F_3 generation and will continue to produce them as long as it is inbred The two heterozygotes will split up in the F_3 generation in the same 1 2 1 ratio as did their hybrid parents of the F_2 generation The recessive homozygote will produce only recessive homozygotes as long as it is kept pure by being inbred

It is interesting to consider what will happen if a heterozygote form is crossed with a homozygous recessive It should be obvious that one half of the progeny would be pure recessives, while the other half would be heterozygotes, that is, there would be a 1 1 ratio A similar result would be obtained by crossing a heterozygote with a dominant homozygote, although all the immediate progeny would show the dominant character The real situation would be revealed, however, when this progeny was inbred, for one-half would be homozygous (pure breeders) and the other half would be heterozygous (hybrid breeders)

Thus far we have considered only what is called the monohybrid ratio, that is, the ratio obtained from one pair of contrasting characters, such as tallness and dwarfness The next step is to consider the dihybrid ratio Mendel also used contrasting seed characters finding, for example, that smoothness in seeds is dominant to a wrinkled condition Introducing this pair of contrasting characters into the situation we have been considering, the dihybrid ratio will be the result Crossing a tall smooth seeded individual with a dwarf wrinkled seeded individual it is evident that all of the F_1 or first hybrid generation will be tall, smooth seeded individuals, since both of these characters are dominant In the F_2 generation, however, the following ratio will appear 9 tall smooth 3 dwarf smooth 3 tall wrinkled, 1 dwarf wrinkled, which is a 9 3 3 1 ratio This is the dihybrid ratio, the explanation of which may be indicated in Figure 57 The question may be raised why the characters for tallness and smoothness are not represented on the same chromosome If they were, the result would be a *simple monohybrid ratio*, except that the tall individuals would always be smooth seeded as well and dwarfs would be always wrinkled seeded The possibility of one chromosome carrying two different determiners will be considered later, but at present we shall assume that these determiners are on different chromosomes

Figure 57 shows that we are dealing with two homozygotes each producing only one kind of gamete, so that all the hybrid progeny will be similar, both genotypically and phenotypically, that is with the same germinal constitution and the same appearance By inbreeding these F_1 individuals it will be seen that four kinds of gametes are involved Crossing these four kinds of gametes the resulting combinations are indicated in Figure 57 The result is four phenotypes as follows Nos 1, 2, 3, 4, 5, 7, 9 10, 13 are tall smooth individuals Nos 11, 12, 15 are dwarf, Nos 6, 8, 14 are tall wrinkled, No 16 is dwarf wrinkled This is the 9 3 3 1 ratio

It will be noticed that Nos 1, 6, 11, 16 are homozygotes and therefore will breed true, but the rest are heterozygotes either for one pair of characters or for both, and these would split into various types upon further breeding

The next step is the trihybrid ratio Mendel found yellow seeds dominant over green seeds, and if this pair of characters is included with those used above the trihybrid result can be observed The experiment would consist in crossing tall, smooth, yellow individuals with dwarf, wrinkled, green individuals, and it is obvious that the

hybrid progeny would all be tall smooth, yellow, since these three characters are dominant Inbreeding the hybrids gives the following result in the F_2 generation 27 tall smooth yellow, 9 tall smooth green,

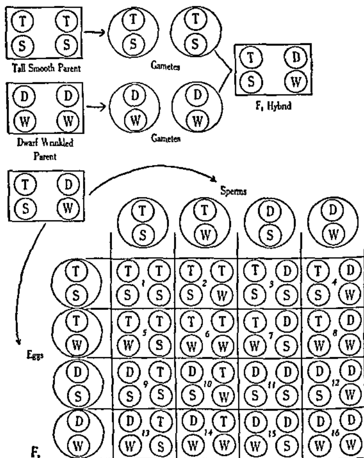


FIG 57 —Diagram illustrating dihybrid ratio Upper part shows how original parents were crossed to give F_1 hybrid lower part shows F_1 hybrid producing four kinds of gametes chance matings among these gametes when F_1 is inbred result as indicated in the large set of squares and explains the 9 3 3 1 ratio in the F_2 generation (*From Coulter and Coulter*)

9 tall wrinkled yellow, 9 dwarf smooth yellow, 3 tall wrinkled green, 3 dwarf smooth green, 3 dwarf wrinkled yellow, 1 dwarf wrinkled green The trihybrid ratio therefore is 27 9 9 9 3 3 3 1 This involves 64 individuals and 8 phenotypes

ILLUSTRATIONS OF SIMPLE MENDELIAN INHERITANCE IN BOTH ANIMALS AND PLANTS[1]

J ARTHUR THOMSON

How far has Mendel's experience been confirmed?—There has been confirmatory work by Correns (on peas maize, and garden stock), by Tschermak (on peas), by De Vries (on maize, etc), by Bateson and his collaborators (on a large variety of organisms), by Darbishire (on mice), by Hurst (on rabbits), by Toyama (on silk moths), by Davenport (on poultry), and so on There are some difficulties and not a few discrepancies, but, as Bateson says "the truth of the law enunciated by Mendel is now established for a large number of cases of most dissimilar characters "

In experimenting with *Lychnis*, *Atropa*, and *Datura*, Bateson and Saunders found that the phenomena conformed with Mendel's law 'with considerable accuracy, and no exceptions that do not appear to be merely fortuitous were discovered. In the case of *Matthiola* (garden stock), the phenomena are much more complex There are simple cases which follow Mendelian principles but others of various kinds which apparently do not The latter cases fall into fairly definite groups, but their nature is obscure "

In experiments with poultry, the phenomena of dominance and recession were detected, interbreeding of the hybrid offspring resulted in a mixed progeny, "some presenting the dominant, others the recessive character, in proportions following Mendel s Law with fair consistency, though in certain cases disturbing factors are to be suspected "

The general result, so far, is that Mendel's law has received confirmation in a number of very dissimilar cases

Dominant and recessive characters—Let us first of all collect a number of instances of contrasted characters which behave in relation to one another as dominants and recessives

	Dominant	Recessive
Pisum sativum	Tallness	Dwarfness
	Round seeds	Wrinkled seeds
	Coloured seed-coats	White seed-coats
	Yellow albumen in cotyledons	Green albumen in cotyledons
	Purple flowers	White flowers
Sweet pea	Tall ordinary form	Dwarf or cupid variety

[1] From J Arthur Thomson, *Heredity* (copyright 1907) Used by special permiss on of the publisher John Murray London.

	Dominant	Recessive
Stocks	Coloured	White
Wheat and barley	Beardless	Bearded
	Later ripening Rivett wheat	Early ripening Polish wheat
	Non immune to rust	Immune to 'rust
Maize	'Starch seed	Sugar seed
Nettles (*Urtica pilulifera* and *U dodartii*)	Serrate leaf margin	Entire leaf margin
Mirabilis jalapa and *M rosea*	Rose colour	Other colours
Mice	Coloured coat	Albino coat
	Normal	Waltzing variety
Rabbits	Coloured coat	Albino coat
	Angora fur	Short fur
Poultry	Rose comb of Hamburghs and Wyandottes	High serrated single comb of Leghorns and Andalusians
Cattle	Hornlessness	Horns
Snails	Bandless shell	Banded shell

Other instances in plants —As is well known, there are two almost equally common forms of wild primrose (A) thrum types, with short styles and with anthers at the top of the corolla tube, and (B) pin types, with long styles and with anthers half way down the tube The thrum type is dominant over the pin type

The original species of Chinese primrose (*Primula sinensis*) has a palmate leaf About 1860 a sport arose (from seed) which had a pinnate or "fern" leaf The palmate form is dominant, and the fern leaf is recessive

The deformed ' Snapdragon" variety of sweet pea behaves as a recessive to the normal type.

The 2 row barley has certain lateral flowers which are exclusively staminate in 6 row barley all the flowers are staminate and pistillate and all set seed Mr Biffen crossed these forms, and found that the more negative character was dominant The offspring were 2 rowed

Maize —When the common or starchy round seeded maize is crossed with the wrinkled seeded sugar maize, the round starchy character dominates When an egg-cell of the wrinkled sugar maize stock is fertilised by a pollen cell of the round starchy stock the result is a round seed with starchy endosperm If this seed is sown, it becomes a plant which, on self fertilisation, forms a cob with a mixture of round starchy and wrinkled sugary seeds in the ratio 3 1 The wrinkled seeds yield sugar maize, the round seeds yield two "impure rounds' to one "pure round" Correns has observed a very interesting case in which two pairs of contrasted characters are implicated

One variety, *Zea mays alba*, which has *smooth* white seeds, was crossed with another variety, *Zea mays coeruleodulcis*, which has wrinkled *blue* seeds The hybrids (F_1) had *smooth blue* seeds, one character of each parent being dominant, and one character of each parent being recessive. The hybrids were inbred, and the progeny (F_2) showed four combinations—*smooth blue*, *smooth* white, wrinkled *blue*, and wrinkled white (the dominant characters are italicised)

In the next generation (F_3), the wrinkled white, inbred, yielded wrinkled white—a case of extracted recessives, breeding true The *smooth* whites and wrinkled *blues*, inbred, yielded partly forms like themselves and partly wrinkled white The *smooth blues*, inbred, yielded the same combinations as in F_2

A finer corroboration of Mendelian could hardly be wished.

Nettles —Correns crossed two 'species of stinging nettle,' *Urtica pilulifera L* and *U dodartii L*, which resemble one another except as regards leaf margin, strongly dentate in the former, almost entire in the latter The hybrid offspring (F_1) have all dentate leaves like the male or the female parent, as the case may be The dentate character is absolutely dominant The inbred (self fertilised) hybrids produce offspring (F_2) of two kinds, with dentate and with entire margins, on an average in the Mendelian proportion, 3 1

"Immunity to rust in wheat.—Some kinds of wheat are very susceptible to the fungoid disease known as 'rust', others are immune The quality of immunity to rust is recessive to the quality of predisposition to rust

'When an immune and a non immune strain are crossed together the resulting hybrids are all susceptible to 'rust' On self fertilisation such hybrids produce seed from which appear dominant 'rusts and recessive immune plants in the expected ratio of 3 1 From this simple experiment the phrase 'resistance to disease' has acquired a more precise significance, and the wide field of research here opened up in this connection promises results of the utmost practical as well as theoretical importance To the question Who can bring a clean thing out of an unclean?' we are beginning to find an answer, nor is the answer the same as that once given by Job (R C Punnett)

Silkworms —Toyama paired Siamese silkmoths with yellow or with white cocoons the offspring produced only yellow cocoons When the hybrids were inbred the result was two sets, one producing white cocoons, the other producing yellow cocoons and the proportion was Mendelian—25 037 white and 74.96 yellow The whites bred

true, the yellows when inbred showed themselves to be pure dominants or "yellows" and dominant recessives—i e, splitting up again into yellows and whites in the usual proportion More intricate experiments confirmed this general result

It must be noted, however, that Coutagne has made much more elaborate experiments with different results, which in *many* cases can not be interpreted on the Mendelian theory Thus he found (1) that the hybrid forms were sometimes blends of the parents and different from both (2) that in other cases the brood included some like one parent in a particular character, some like the other parent, and some intermediate, and (3) that in other cases the individuals showed no fusion of characters, but resembled one or other parent It is likely that the discrepancy may be explained as due to considerable diversity of origin in the domesticated races of silkworm, so that, while they breed true when left to themselves, a disturbance of the usual routine leads to the liberation of latent characters

Lina lapponica —Miss McCracken has made a fine study of the hereditary relations in this Californian beetle, which occurs in two types, spotted (dominant) and black (recessive) They are always crossing in natural conditions, but there are no intermediates, and it is easy by isolation to rear a "pure" spotted race and a "pure" black race When spotted forms are paired they may produce only spotted progeny—a case of extracted dominants In other cases, however, they yield spotted and black forms (1,021 spotted, 345 black), i e, in the Mendelian proportion of 3 1—a case of dominant recessives inbred

Snails —Lang paired "pure" five banded forms of the common or garden snail, *Helix hortensis*, with bandless forms from bandless colonies The young of the first generation were all bandless, the banded character being recessive When these were paired the off spring were bandless and banded in the Mendelian ratio, 3 1 Further experiments confirmed this, not only as regards bands, but also as regards colour (yellow or red), size, and the form of the umbilicus *It may be said, therefore, that common snails (Helix hortensis and Helix nemoralis) illustrate Mendelian inheritance*

Poultry —Numerous breeding experiments with poultry have been made by Bateson, Bateson and Punnett, Hurst, Davenport and others, many of which show Mendelian phenomena with great clearness, while others are strangely conflicting One of the reasons for the complicated results is evidently to be found in the difficulty of securing thoroughly "pure" breeds, for many that breed true as long as they

are inbred tend to liberate latent characters when the ordinary course of breeding is departed from.

Hurst contrasts the following characters which usually show themselves dominants and recessives but it has to be admitted that the dominance—always complete for some characters—is for others frequently, or even always incomplete—i.e, showing traces of the corresponding recessives.

Dominant Characters	Recessive Characters
Rose comb	Leaf comb single comb
White plumage	Black plumage, buff plumage
Extra toes	Normal toes
Feathered shanks	Bare shanks
Crested head	Uncrested head
Brown eggs	White eggs
Broodiness	Non brood ness

Davenport s copiously illustrated work is also of great interest He shows in case after case that the character dominant in the first hybrids is more or less influenced by the recessive character Polish fowls with a large hernia of the brain on the top of the head were paired with Minorcas with normal heads The hybrids showed no hernia but most of them showed a frontal prominence When the hybrids were inbred the hernia occurred in 23 5 per cent—a close approximation to the theoretical 25 per cent.

Single combed black Minorcas were crossed with white-crested black Polish fowls with a very small bifid comb The hybrids had combs single in front split behind When the hybrids were inbred there resulted in a total of 101 offspring 29 7 per cent with single combs (like Minorcas) 46 5 per cent with Y-shaped combs and 23 8 per cent with no combs or only papillae (like the Pol sh forms) Here again the result is in a general way Mendelian but the Y like comb is a complication

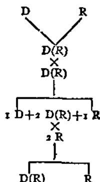
Pigeons —R Staples-Browne crossed a web footed pigeon (an occas onal discontinuous variation) with a normal form and got six normal young In other words the web foot character is recessive to the normal foot character The hybrids were inbred and in one case produced nine with normal feet and three with webbed feet—a Mendelian splitting up But from another pair of hybrids seventeen *normal offspring resulted Thus the illustration of Mendelian* inheritance is inconclusive Besides the numbers were too small

We have noticed elsewhere that crossing different breeds of pigeons often results in forms which more or less resemble the reputed original

ancestor, the wild rock dove, in other words, reversions occur Often, however, the results seem quite anomalous which is probably due to the number of latent characters which different races of pigeons appear to carry

Mice —Mendelian phenomena have been carefully studied in mice. Thus when a grey mouse is paired with an albino, the hybrid offspring are always grey When these are inbred, they yield greys and albinos approximately in the proportion of 3 1 Thus Cuenot obtained 198 grey, and 72 albinos.

Darbishire has obtained many results which harmonise well with Mendelian theory while others require some ingenuity if they are to be fitted in with this interpretation As a good case we may cite one where the inbreeding of pigmented mice—derived from crossing pigmented and albino individuals—yielded 159 pigmented young and 55 albinos (53 5 being the theoretical anticipation) When similar hybrids were paired with pure albinos they yielded 69 pigmented and 69 albino forms, precisely as the theory would lead us to expect



Cuénot crossed an albino AG (with latent grey) with an albino AB (with latent black), and obtained albinos (AGAB) He crossed a black mouse CB with an albino AY (with latent yellow), and obtained yellow mice (CBAY) He then paired AGAB (albino) with CBAY (yellow) and obtained 151 young—81 albinos, 34 yellow, 20 black, 16 grey, the theoretical anticipation being —76 albinos 38 yellow, 19 black, 19 grey This is an exceedingly striking and convincing case

Waltzing mice —The mice of this interesting Japanese breed have among other peculiarities the habit of waltzing round in circles When waltzing mice are crossed with normal mice their abnormal quality behaves as a recessive

Guinea-pigs—If a black guinea pig of pure race be crossed with a white one the offspring will be all black, and if these are mated with each other the recessive white character reappears on the average in one in four of their offspring These whites mated with each other produce only white offspring, while the black are as usual of two kinds, pure blacks and impure blacks. Similarly, as Professor Castle has shown, a rough coat is dominant over a smooth coat, and a short coat over a long coat.

Rabbits—Hurst paired white Angora rabbits (with pink eyes and silky hair) with "Belgian hare" rabbits (with pigmented skin, dark eyes, and short yellow fur) The hybrids were pigmented like the "Belgian hares," but the fur was grey like that of the wild rabbit. These hybrids were inbred, and 14 distinct types resulted—an apparent "epidemic of variation" to which Mendel's theory has supplied the clue, for four pairs of contrasted characters are involved in the hybrid inbreeding—namely, short hair versus long hair, pigmented coat versus albinos, grey versus black coat, uniform versus marked coat (Dutch marking latent in the albinos), and the 14 distinct types illustrate the possible combinations.

As regards short hair versus long hair, Hurst found that when the short-coated hybrids were inbred they produced short haired forms like the Belgian hare grandparent, and long haired forms like the Angora grandparent Out of 70 which reached the age of two months or more, 53 were short haired and 17 long haired—a close approximation to the Mendelian anticipation, 52 5 17 5 Similarly, as regards pigmented coat versus albino, the hybrids, when inbred, yielded 132 pigmented and 39 albino forms—a close approximation to the Mendelian expectation, 129 43, and so on

Cats—There are some interesting results as to colour (Doncaster) Thus, "pure orange ♀ crossed by "pure" black ♂ gives tortoiseshell females and yellow males, but black crossed by orange gives black males or females, tortoiseshell females, and orange males It seems that orange usually dominates over black in males, while in females the orange (for some unknown reason) is less dominant and tortoiseshell results Male tortoiseshell cats are very rare In this case the results are complicated by some peculiarity wrapped up with "sex

When a male tortoiseshell is paired with a female tortoiseshell the *kittens are tortoiseshell, orange, and black*—which is what Mendelian theory would lead us to expect

Man—Evidence of Mendelian phenomena in man is as yet very scanty It appears that the condition known as brachydactylism

where the fingers are all thumbs with two joints instead of three, is dominant over the normal In five generations chronicled by Farabee about half of the offspring were of the abnormal type, though the marriages were apparently always with unrelated normal individuals Moreover, no normal member of the lineage is known to have transmitted the abnormality Another good case has been recently discussed by Drinkwater

Of great interest also is Mr Nettleship's account of the descendants of one Jean Nougaret (born 1637), who was afflicted with "night blindness"—a condition apparently due to loss of visual purple It seems to behave like a unit character There are records of over 2,000 individuals, and the night blindness is dominant over normal eyesight. The notable point is that during two and a half centuries no normal member of the lineage who married another normal, whether related or not, ever transmitted the disease

Human eye colour affords another illustration. It is largely determined by the presence or absence of two distinct layers of pigment In the true blue eye only one of these pigmentary layers is visibly present, the posterior purple pigment of the choroid, which, being reflected through the fibrous structure of the iris, produces the blue colour In the absence or partial absence of this pigment the eye appears to be "pink," as in albinos In the ordinary brown eye two layers of pigment are present, for in addition to the posterior purple layer there is also an anterior brown layer, in front of the iris Major C C Hurst found that the eye with two layers of visible pigment (duplex) is dominant and the eye with one layer of visible pigment (simplex) recessive Or, putting it in another way, the presence of the brown front layer is dominant to its absence. Practically the same conclusion was reached independently by Professor and Mrs Davenport

The Davenports and Major Hurst have also brought forward some evidence illustrating in typical Caucasians the dominance of dark to fair skins, their segregation in the same family, and the apparent purity of the extracted fair individuals Hurst also gives evidence that 'fiery red hair behaves as a recessive to brown, and that the musical sense or temperament is also recessive It seems as if an individual is non musical owing to the presence of an inhibitory factor preventing the expression of musical temperament which is potentially present in everyone (Hurst 1912)

It would be interesting to have precise information as to the progeny of Eurasians who intermarry, for here the original hybrids result from the mixture of two very distinct races

CHAPTER XIX

THE FACTOR HYPOTHESIS AS APPLIED TO PLANTS

JOHN M COULTER AND MERLE C COULTER

Thus far we have been considering Mendel s law in its simple form and have enlarged but little upon Mendel s original statement The value of the law is apparent Upon its republication in 1900 it was taken up by biologists and numerous breeders set to work to test it As a consequence data for and against it began to accumulate. As might be expected there was much apparent evidence against the law but as geneticists developed a better conception of the mechanism the contradictory evidence was explained away Almost every type of inheritance has now been explained according to Mendel s law Some of the explanations are very complicated and cannot be in cluded in this presentation A few of the more important cases however will be presented

I PRESENCE AND ABSENCE HYPOTHESIS

This may be regarded as a new method of Mendelian thought. It was first suggested by Correns but later was worked out in detail by other geneticists especially Hurst Bateson Shull and East It is merely a modification of the mechanism involved For example in the case of a hybrid obtained by crossing tall and dwarf parents the result had been explained as due to the fact that one chromosome bears a determiner for tallness and the other one of the pair carries the deter miner for dwarfness In other words each one of a pair of allelomorphs is represented by a determiner two determiners thus being present Dwarfness in this case would be the result of the interaction of that determiner and its environment during the development of the body and the same for tallness When both were present however, the conception of the situat on was as follows The determiner for dwarfness setting up its usual series of reactions early became para lyzed by the determiner for tallness or its products This result was called the dominance of the character for tallness It was as if the determiner for tallness completely prevented the activity of the deter miner for dwarfness This conception was apparently borne out

From Coulter and Coulter *Plant Genetics* (The University of Chicago Press. copyright 1918)

by the facts and was the explanation of the mechanism generally accepted

According to the presence and absence hypothesis, however, the situation is looked at from an entirely different point of view Tall ness is the result of a determiner but dwarfness is merely the result of the absence of the determiner for tallness The dominant character is produced by an inheritable determiner but the recessive character appears only when the dominant determiner is lacking This con ception has some evident advantages and may modify the previous Mendelian diagram as shown in Figure 58 This appears to be a simpler mechanism to account for the phenomenon called dominance In the case of the dwarf form there is a normal course of development, in the case of the tall parent or hybrid, however, an additional determiner

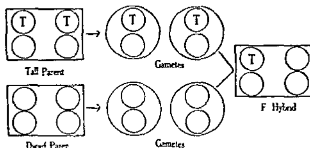


FIG 58—Diagram showing how the original scheme must be modified to satisfy the presence and absence hypothesis (*From Coulter and Coulter*)

stimulates cell growth or cell division or both It is a simpler and more useful conception so long as it fits the facts Some investigators however claim that it cannot be applied to all the situations that have been discovered

[It should be emphasized here that the word "determiner" as used in the foregoing paragraphs is not synonymous with the word "gene" A recessive character is not due to the absence of a gene but merely to the absence of something that is present in the dominant gene In this form the presence and absence idea is acceptable]

Additional advantages of the presence and absence hypothesis will appear in connection with a consideration of blending inheritance and of cumulative factors in inheritance Attention however, should be called to the fact that those who accept the presence and absence

hypothesis do not use the form of notation thus far used in explaining Mendelian inheritance Assume that T is used to express the determiner for tallness its same letter (t) is used to express the absence For example, instead of using D for dwarfness, t is used for 'lack of tallness' (Fig 59) It is a matter of convenience to have a symbol to represent the recessive, the absence of something that is present in another individual

In summary the essential difference between the presence and absence hypothesis and that of dominant and recessive is that in the former case the recessive determiner has no existence at all while in the latter case it exists but is in a latent condition when associated with the dominant

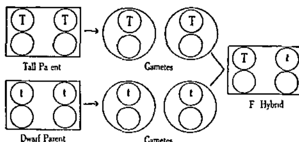


FIG 59—Diagram showing how presence and absence scheme is actually used with small letter representing absence (*From Coulter and Coulter*)

II BLENDS

This type of inheritance when first discovered was thought to be in direct conflict with Mendel's law It is a case in which dominance seems to fail, for the two alternative characters both express themselves and the result is an average between them It is easy to explain this situation in accordance with the presence and absence hypothesis without any violation of Mendel's law

The classic example of blending inheritance was presented by Correns in breeding work upon *Mirabilis Jalapa*, the common four-o clock Correns crossed red and white varieties, and all the hybrid progeny had rose pink flowers This was a color blend, distinctly intermediate between the colors of the two parents The F_1 generation, therefore seemed to contradict Mendel's law in that one color character was not completely dominant over the other The real situation however, appeared in the F_2 generation obtained by inbreeding

individuals of the F_1 generation which showed the blend By in breeding the pink hybrids Correns obtained the perfect 1 2 1 ratio, that is 1 red like one grandparent, 2 pink like the hybrid parent, and 1 white like the other grandparent Segregation was evidently taking place, the only unusual thing being the *appearance* of the F_1 individuals, and that was explained immediately as failure of dominance (see Fig 60)

The question this introduces, therefore, is that of a mechanism which could account for such a result. The easiest explanation offered is that the red parent was a homozygote for redness (double dose) and the hybrid a heterozygote (single dose), the inference is that

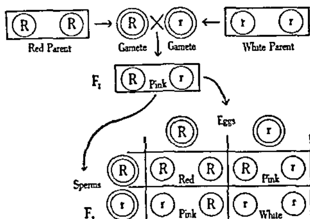


FIG 60—Diagram illustrating blending inheritance discovered by Correns in *Mirabilis jalapa* (*From Coulter and Coulter*)

a single dose produces pink while a double dose produces red A theoretical explanation of this occasional difference in the result of double and single doses is as follows Imagine that the body cells of a plant have a certain capacity for expressing hereditary characters In such a case, just as a given quantity of solvent can dissolve only a given amount of solute, so the body cells can express hereditary characters only to a definite limited extent. In the four-o'clock a single dose of redness may be thought of as half saturating the body cells, while a double dose completely saturates them In cases showing complete dominance, however, a single dose completely saturates the cells and a double dose can do nothing more This analogy assists in visualizing on the one hand the necessary mechanism of blends (apparent failure

of dominance) and on the other hand that for cases of complete dominance

Another example of simple blending inheritance is the case of Adzuki beans described by Blakeslee In this bean the mottling of the seed coat is dominant to the lack of mottling In the hybrid condition however, the mottling is lighter than in the pure or homozygous condition Heterozygous plants therefore can be easily distinguished from homozygous plants so that the 1 2 1 ratio is evident on external inspection rather than the usual 3 1 ratio

III THE FACTOR HYPOTHESIS

Mendel concluded that each plant character depends upon a single determiner Inheritance however has proved to be a much more complex phenomenon than indicated by Mendel s peas Ratios have appeared that were puzzling and geneticists were forced to the conclusion that there may be a compound determiner for a single character This conception is called the *factor hypothesis* and the growing complexity of genetics has developed in connection with this hypothesis With the consideration of *factors* instead of *determiners* one passes from elementary to advanced genetics Previously we have used the word determiner implying Mendel s idea that a single determiner is responsible for the development of a plant character and this has been true of the examples of inheritance previously considered It is understood now however that a character is frequently determined by the interaction of two or more separately heritable factors and hence the factor hypothesis The distinction between factors and determiners should be made clear In case only one factor is involved in determining a character there is no distinction between factor and determiner and in such a case the term factor should not be used

1 Complementary factors —This is the simplest expression of the factor hypothesis and it may be illustrated by some of East s work Crossing red grained and white-grained corn he obtained all red in the F_1 generation This would suggest that the F_2 generation would show 3 red to 1 white but it showed 9 reds to 7 whites which did not suggest Mendelian inheritance It is in accord with Mendel s law however if we consider that two complementary factors are necessary to produce the red character and that each of these factors is inherited separately Such a situation would give a dihybrid ratio as indicated in Fig 61 It will be seen that out of 16 progeny 9 will be red for they alone contain the complementary factors, the other 7 will be white

The situation is thus explained by the dihybrid ratio, but although only one character is involved that character depends upon two complementary factors

Another situation is worth noting No 6 of the diagram is white because it contains only one of the necessary factors, No 11 is white

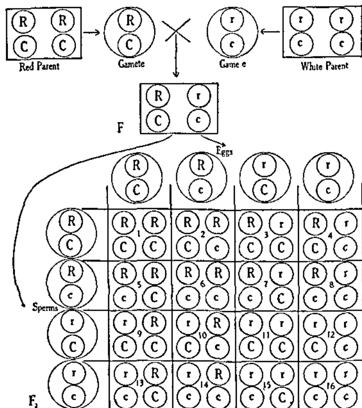


Fig 61 —Diagram illustrating behavior of complementary factors in cross between red grained and white grained corn *R* and *C* must both be present to produce red-grained corn (*From Coulter and Coulter*)

for the same reason, but its germinal constitution is just the opposite What would happen if these two are crossed? There is only one possibility, since each is a homozygote producing only one kind of gamete The result would be red, and thus a cross between two whites would produce only reds What would happen from crossing Nos 6 and 15, the former being a homozygote and the latter a heterozygote?

It is obvious that the resulting progeny would be one-half white and one-half red although both parents are white The same result would be secured in crossing Nos 11 and 14 A cross between Nos 14 and 15 both of which are heterozygotes would result in 3 whites and 1 red the ordinary 3 1 ratio These illustrations show how differently the same phenotype may behave in inheritance In each case two whites were crossed that is the same phenotypes but three different ratios were obtained because the genotypes were different

The striking feature of this situation is that one can cross two whites and get a red This gives an insight into the so-called phenomenon of *reversion* For example in the course of numerous breeding experiments Bateson obtained two strains of white sweet peas each of which when normally selfed bred true to the white color but when these two were artificially crossed all the progeny had purple flowers like the wild Sicilian ancestors of all cultivated varieties of the sweet pea This appeared to be a typical case of reversion Further breeding however showed that this was just such a case of complementary factors as we have been considering One of Bateson s white strains had one of the factors for purple and the other strain had the other factor

Complementary factors have been defined and the method of their inheritance described but is there any mechanism to explain the situation? A suggestion may be obtained from plant chemistry The most prominent group of pigments in plants is the group of anthocyanins which are produced as follows Plants contain compounds called chromogens which are colorless themselves but which produce pigments when acted upon by certain oxidizing enzymes or oxidases This is a sufficient mechanism for the behavior of complementary factors If one of East s white strains of corn contained a chromogen capable of producing red but lacked the necessary oxidase it would remain colorless If the other white strain contained the oxidase but no chromogen it would remain colorless In crossing them however chromogen and oxidase would be brought together and a red grained hybrid would be the result Inbreeding such red grained individuals of course would give red and white progeny in a ratio of 9 7 as explained in connection with East s corn This seems to be the explanation of the behavior of complementary factors in many cases of color inheritance

Where other characters are involved the mechanism must be somewhat different In some cases the two factors may be the enzym•

and the compound the enzyme attacks, as in the oxidase and chromogen situation just described On the other hand, we might be dealing with two chemical compounds that are inert when occurring separately but active when brought together, active in such a way as to produce a distinctly new character Also two active substances might neutralize one another when brought together in a hybrid, and the failure in their activity might result either in a new character or the failure of some parental character to develop Such are some of the possible mechanisms to explain the behavior of complementary factors

Hybridizing therefore is much like mixing chemicals in a test tube We know that very wide crosses cannot be made successfully but the surprising thing is that certain very close crosses are constantly unsuccessful, even though both parents may cross freely with closely related types We obtain a glimpse of the possibility of such apparently inconsistent behavior when we consider the chemical possibilities suggested by the behavior of complementary factors

The origin of complementary factors is an interesting field of speculation Did they originate together or separately? A natural inference would be that they originated together, for neither would be of any use without the other It should be remembered, however that the idea of use as explaining the occurrence of everything in a plant is being abandoned one must think rather of a plant as a complex physico-chemical laboratory No one claims that all chemical reactions are useful they are simply inevitable and plant characters are the result of chemical reactions and physical necessities Even though we assume the simultaneous origin of two complementary factors they would have to be put on separate chromosomes for the factors are separately inherited

The other alternative is to suppose that these factors originated independently in the history of a plant In this case, of course the first one to be produced would remain functionless until finally its complement came into existence This might be an explanation of what are called latent characters Also they might have not only originated independently but in different varieties or species In this case if natural hybridizing should bring them together the result would be the appearance of a new character, and this may have been a very important factor in the origin of species

This may serve as an introduction to the factor hypothesis with complementary factors as an illustration simply because it is the simplest situation There are many other kinds of factors recognized

but we shall not attempt to list all of the proposed types A simple illustration of the better known types is as follows

a) A *complementary* factor is added to a dissimilar factor to produce a particular character

b) An *inhibitory* factor prevents the action of some other factor

c) A *supplementary* factor is added to a dissimilar factor with the result that the character is modified in some way

d) A *cumulative* factor, when added to another similar factor, affects the degree of development of the character

Some examples of these types will make them clear, those for complementary factors having been given previously

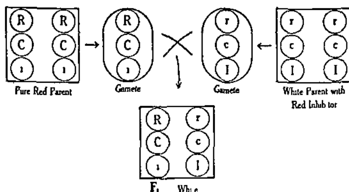


FIG 62 —Diagram illustrating behavior of inhibitory factor (*From Coulter and Coulter*)

2 Inhibitory factors —Recalling East s experiment with red grained corn it will be remembered that when both factors for red were present the grain was red, but when either factor was absent the grain was white Later he crossed these strains with a new white strain, and the result was surprising The pure red strain produced gametes carrying both the red factors, and it would be expected that whatever such a gamete mated with would result in red progeny, but when this pure red was crossed with the new strain of white the progeny were all white, although the hybrids certainly contained both factors for red The explanation which first occurred to East, and which later experiments confirmed, was that the new white strain contained an inhibitory factor, which prevented the development of red even though both the complementary factors for red were present

Figure 62 illustrates the situation and shows why all the individuals of the F_1 generation are white It is interesting to note further the possibilities of white and red in the F_2 generation They would be

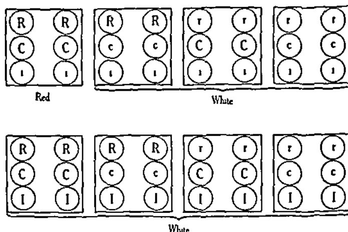


FIG 63 —Diagram showing some possible combinations in F_2 when F_1 of Figure 62 is inbred Individual on left end of upper set red grained because *R* and *C* both present and *I* absent other individuals in upper set white because lacking *C* or *R* or both individuals in lower set with inhibitory factor and therefore white whatever other combinations of factors they may contain (*From Coulter and Coulter*)

numerous since we are dealing with trihybrid ratios (see Fig 63) This does not exhaust the possibilities, for the cases given were homozygotes, each producing a single kind of gamete There remains for consideration the heterozygote situation (see Fig 64)

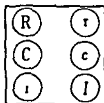


FIG 64 —(*From Coulter and Coulter*)

The possible mechanism of the inhibitory factor is as follows We have assumed that red is produced only when the enzyme is present to oxidize the chromogen Enzymes are very sensitive, their activities may be affected or completely checked by various agents Suppose that *I* of the diagram be such an agent and the necessary mechanism is apparent When *I* is present *R* is paralyzed, so that it cannot oxidize *C*

3 Supplementary factors —A supplementary factor is one that is added to a dissimilar factor, with the result that a character is modified in some way

In his work upon red grained races of corn East found occasionally a few purple grains His conception of the situation is as follows The pure red plant contains two complementary factors, one (*C*) a chromogen, and the other (*R*) an enzyme, which when brought together produced the red color The purple grains, however, must be explained by the presence of still another factor (*P*) the resulting situation being represented in Figure 65 Of course when *C* is absent no pigment whatsoever can be produced As a consequence we will assume that the presence of *C* is constant, and that *P* and *R* are variables For a similar reason we will assume that the absence of *I* is constant The figure shows three possibilities, from which the following conclusions may be drawn (1) when *P* and *R* are both present the result is purple grains, (2) red appears only in the absence of *P*, (3) *P* although present will not develop any color in the absence of *R*

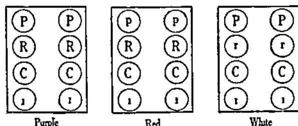


FIG 65 —Diagram illustrating action of supplementary factor (*From Coulter and Coulter*)

This is a typical case of a supplementary factor, that is, one which is added to a dissimilar factor, with the result that the color character is modified The mechanism of this situation will make clearer the behavior of the supplementary factor If *C* is the chromogen and *R* the enzyme, what is *P*? The suggested answer can be obtained from plant chemistry It is found that the purple pigment is produced by the same substance as the red, but represents a higher state of oxidation The conclusion is obvious *C* is oxidized by *R* up to a certain point, where red is produced, but if *P* is also present it represents an additional enzyme, which attacks the red pigment and oxidizes it still further into purple *P* is incapable of attacking the original chromogen, but when *R* carries the attack to a certain point, *P* can function and carry the oxidation further As a consequence *P* without *R* gives white grains, while *R* gives red grains only in the absence of *P*.

4. Cumulative factors —These will be considered under the next heading, "Inheritance of quantitative characters"

In addition to the four types of factors given, the literature of genetics also contains discussions on intensifying factors, diluting factors, distribution factors, etc These, however, do not introduce any new mechanisms

5 Inheritance of quantitative characters —This phase of the factor hypothesis if true is of fundamental importance not only to genetics but to general biology It is based upon the conception of cumulative factors and as it is presented it will be realized that it throws light not only upon numerous breeding experiments but also upon variation in general, which means evolution also A cumulative factor was defined as one which, when added to another similar factor, affects the degree of development of the character

It will be recalled that Correns crossed red and white strains of *Mirabilis* and obtained pink hybrids The suggested explanation of this result was that a single dose of the red determiner gives pink while a double dose gives red When Correns inbred these pink hybrids he obtained the result presented in Figure 60, that is, 1 red, 2 pink, 1 white This result is obvious and the mechanism is plain

With this diagram in mind we shall consider some of the experiments of Nilsson-Ehle at the Swedish Experiment Station He crossed two strains of wheat with red and white kernels The F_1 individuals had light red kernels which of course suggests a repetition of the situation shown by *Mirabilis* in the experiment of Correns The F_2 generation, however, showed a very different result The reds and whites appeared in the ratio of 15 1, but in addition to this, among the 15 reds there could be distinguished varying degrees of redness Nilsson Ehle suspected that 15 1 meant a dihybrid ratio 16 individuals being necessary to give the ratio so that he constructed the tentative scheme shown in Figure 66

This shows a regular dihybrid ratio, except that the two factors involved are similar Applying the single dose and double dose conception, as used in the case of Correns pink *Mirabilis*, we reach the following conclusions No 1 only has four doses and therefore it only is deep red, Nos 2, 3, 5, 9 have three doses and are somewhat lighter red, Nos 4, 6, 7, 10, 11, 13 have two doses and are still lighter red, Nos 8, 12, 14, 15 have one dose and are very light red, while No 16 alone has no dose and is the only pure white This accounts for the 15 1 ratio, and the different shades of red This is entirely in

accord with the conceptions that have been presented, and only two assumptions are necessary (1) that dominance is absent, and two doses have twice the effect of one, (2) that the independent similar factors are cumulative in their operation, and are paired with their absence in the hybrid This was Nilsson Ehle's conception, and of

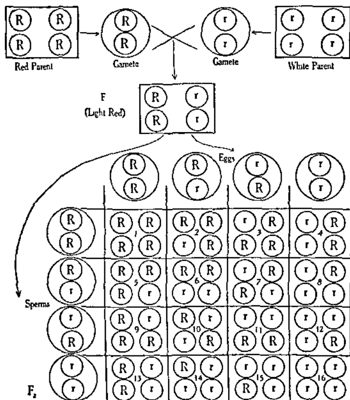


FIG 66—Diagram illustrating Nilsson Ehle's explanation of 15 1 ratio obtained in F_2 generation from cross between red-grained and white grained wheat (*From Coulter and Coulter*)

course he tested it by further experimental work, the results consistently confirming the conception

Since it is important to fix this conception clearly in mind, another type of diagram may represent the facts even more clearly The proportion of individuals showing the various degrees of redness in the F_2 is graphically recorded in Figure 67, each dot representing one dose of the factors in question

Continuing these investigations, Nilsson Ehle next discovered a new strain of red grained wheat, which, when crossed with the pure white strain, yielded F_1 hybrids of intermediate intensity of red as before The F_2 generation however, showed a different situation Reds and whites were obtained in the proportion of 63 1, the 63 reds as before falling naturally into different groups on the basis of degree of redness Applying the same conception as before Nilsson Ehle

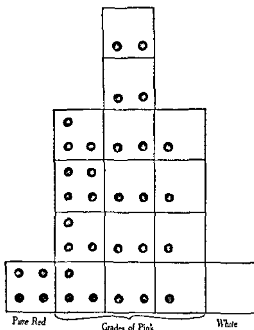


FIG 67 —Another method of visualizing Nilsson Ehle s 15 1 ratio (see Fig 66) (*From Coulter and Coulter*)

discovered that in this case he was dealing with a trihybrid situation Without constructing the usual Mendelian diagram which would have to be extensive enough for 64 individuals, the situation as it appeared in the F_2 generation may be represented by Figure 68 If the graph is surmounted by a curve we recognize the regular ' probability curve," exactly the kind of curve biometricians use to represent the fluctuating individuals about a specific type

This conception of cumulative factors, therefore, has far reaching significance For a long time biologists have recognized individual

variation within the species Darwin depended upon it as the basis of his theory of natural selection as the origin of species, in fact, ever

Pure Red
Intermediate Grades
White

Fig 68 —Diagram illustrating Nilsson Ehle's 63 : 1 ratio (*From Coulter and Coulter*)

since Darwin's *Origin of Species* individual variation has been fundamental in our conceptions To account for this universally recognized phenomenon, Darwin proposed his *transportation hypothesis* as

a possible explanation, which, as will be recalled, did not long survive. Weismann offered in explanation his *germinal selection*, which was soon discarded because it was beyond the possibility of experimental testing. Aside from these two attempts to explain individual variation no other comprehensive scheme had been presented. Biologists had simply recognized the fact of individual variation without any conception of the mechanism. They knew that individual variation existed but had even stopped asking why it existed.

The importance of this new theory, therefore, is obvious. It is an ingenious explanation of the inheritance of quantitative characters and of the existence of individual variations. Furthermore, the theory has not been developed through meditation, but has its basis in scientific experiments. It is imaginative to a certain extent, of course, as is every other valuable theory, but unlike most such theories it has a substantial foundation, namely, Mendel's law.

CHAPTER XX

THE FACTOR HYPOTHESIS AS APPLIED TO ANIMALS

Immediately after the announcement by De Vries in 1900 of the rediscovery of Mendel s paper zoologists in Europe and in America began experiments in animal breeding with the idea of discovering to what extent Mendel s laws were applicable It was soon found that the principles of unit characters dominance segregation monohybrid dihybrid and trihybrid ratios were of practically universal application A number of instances of Mendelian heredity in animals have already been presented in the preceding chapter and no more simple Mendelian cases need be described For a considerable period the animal breeders proceeded no farther in their analysis of the mechanism of heredity than Mendel had done so many years before In time however new facts came to light that needed further analysis and the older Mendelism was superseded by neo-Mendelism This new phase in the study of heredity is in the forefront of interest today Neo-Mendelian heredity in plants has already been discussed It remains for us to present the data on some phases of neo-Mendelism in animals

ILLUSTRATIONS OF THE FACTOR HYPOTHESIS

THE FACTORIAL ANALYSIS OF COLOR IN MICE

Miss Durham after extensive breeding experiments with numerous strains of differently colored mice has been able to show that the appearance of a particular color in an individual mouse is dependent upon the presence or absence of several independently inherited factors evidently represented by genes in as many different chromosomes It seems possible to classify these factors as follows

B = black pigment which masks chocolate pigment
b = absence of B, which gives chocolate

I = intensity factor
i = absence of intensity or dilution factor

C = a complementary color factor acting with P
P = a complementary pigment factor acting with C

If either C or P is absent albino mice result no matter what other color factors may be present

The factorial make up of the various mice in Miss Durham's experiments would, then, be represented as follows

$BICP$ = black
$BiCP$ = blue (dilute black)
$bICP$ = chocolate (absence of black)
$biCP$ = silver fawn (dilute chocolate)

The following experiments indicate the mode of heredity on the factorial basis

1 P Black ($BICP$) × Silver fawn ($biCP$)
F_1 100 per cent Black ($BICP$-$biCP$)
F_2 Black ($BICP$) Blue ($BiCP$) Chocolate ($bICP$) Silver-fawn ($biCP$)
9 3 3 1

2 P Blue ($BiCP$) × Chocolate ($bICP$)
F_1 100 per cent Black ($BiCP$ $bICP$)
F_2 Black ($BICP$) Blue ($BiCP$) Chocolate ($bICP$) Silver-fawn ($biCP$)
9 3 3 1

3 P Blue ($BiCP$) × Silver fawn ($biCP$)
F_1 100 per cent Blue ($BiCP$ $biCP$)
F_2 Blue ($BiCP$) Silver fawn ($biCP$)
3 1

DIFFERENT KINDS OF ALBINOS

Any one of the color types mentioned, if lacking in the factor C, will be an albino though carrying the other factors for color For example, there may be a Black-albino ($BIcP$), a Blue albino ($BicP$), a Chocolate albino ($bIcP$), or a Silver-fawn–albino ($bicP$)

That color factors are present in albinos may be shown by the following experiment An albino had appeared in a Black stock and was crossed with a Silver fawn, thus

4 P Silver-fawn ($biCP$) × Albino extracted from Black ($BIcP$)
F_1 100 per cent Black ($biCP$-$BIcP$)

	Black ($BICP$)	Blue ($BiCP$)	Chocolate ($bICP$)	Albino Black ($BIcP$)	Silver-fawn ($biCP$)
F_2	27	9	9	9	3
	Albino Blue ($BicP$)		Albino Chocolate ($bIcP$)		Albino-Silver fawn ($bicP$)
	3		3		1

The ratios given are the theoretical ratios for a trihybrid Mendelian experiment and the actual results have closely approximated these. As a matter of fact sixteen albinos appeared and it is not possible except by breeding to tell one kind from another. Breeding each with, for example, Silver fawn would readily reveal the differences, for the F_1 generation would all be of the color that is masked by the lack of C in these albinos. In the language of Johanssen there is only one albino *phenotype* but there are four albino *genotypes*. Similarly in experiments (1) and (4) which have just been described the individuals are all Black (phenotypically identical) but that they are not genotypically alike is clearly shown by inbreeding them. In experiment (1) we get only individuals of the four color types, while in experiment (4) we get, in addition to the four color types, four albino types.

FACTORIAL ANALYSIS OF COAT COLOR IN SWINE

Some breeds of swine have a red coat color, as the Duroc Jerseys. Other breeds have a sandy yellowish color. Still others are white. There are other colors but they may be ignored for present purposes. Wentworth has shown that there are two genotypically distinct though phenotypically identical sandy types, the factor analysis being as follows:

$$SSTT - \text{red}$$
$$SStt - \text{sandy}$$
$$ssTT = \text{sandy}$$
$$sstt - \text{white}$$

If this analysis be correct when the two different sandy genotypes ($SStt$ and $ssTT$) are interbred the result would be as follows. All of the F_1 individuals would be red. These when interbred give the following F_2 phenotypic ratio:

$$9\ ST - \text{red}$$
$$3\ St = \text{sandy}$$
$$3\ sT - \text{sandy}$$
$$1\ st = \text{white}$$

The phenotypic ratio is therefore 9 red to 6 sandy to 1 white, which is a rare modification of the 9 3 3 1 dihybrid ratio and is due to the fact that the phenotype sandy, consists of two different genotypes in equal numbers.

COAT COLORS IN GUINEA PIGS

In guinea pigs the wild type coloration is a kind of reddish gray mixture called "agouti" There are also black coat colors and whites (albinos)

Agouti, when crossed with some types of white, gives all agouti in the F_1 generation, and 3 agouti to 1 white in the F_2 generation A black guinea pig crossed with agouti gives all agouti in the F_1, and 3 agouti to 1 black in the F_2 generation Evidently both black and white are recessives to agouti so agouti must be due to at least two dominant color factors *A* and *C*

If we assume that *A* is a dominant factor, whose recessive allelomorph, *a*, gives black color, and that *C* is a dominant factor whose recessive allelomorph *c*, gives white color, then we may put down the formulas for the genetic composition of the three coat colors as follows

$AACC$ = agouti
$AAcc$ = albino (of one kind)
$aaCC$ = black

Then when black ($aaCC$) is crossed with white ($AAcc$), all of the F_1 generation would be agouti and the F_2 ratio would be as follows

9 $AACC$ = agouti
3 $AAcc$ = white
3 $aaCC$ – black
1 $aacc$ = white

This would give a phenotypic ratio of 9 agouti to 3 blacks to 4 whites, another rather slight but unusual modification of the familiar 9 3 3 1 ratio, due to the fact that the phenotype "white" consists of two genotypes

Characters that seemed quite simple at first have been found, by methods similar to those here presented, to be complex when subjected to analysis Such apparently simple characters as human eye color and hair color, though never fully analyzed, would doubtless amply repay investigation If we knew as much about these characters as we do about some animal characters, the testimony of a geneticist in a paternity case would be more valuable than it is at present

CHAPTER XXI

REVIEW OF MENDELISM

At this point it seems well to pause and to take stock of what we have learned about heredity by following Mendel s lead Let us first enumerate some of the rules or laws of heredity discovered by Mendel These are commonly known as *Mendel's laws*

Mendel's first law. the law of dominance —When two parent types differing from each other with reference to a single unit character are crossed, the ' hybrid character resembles that of one of the parent forms so closely that the other either escapes observation completely or cannot be detected with certainty " The character that appears in the first generation hybrids is called "dominant" and that which ap parently becomes latent is called recessive " The law of dominance has been shown to be far from universal in its application In fact, complete dominance is relatively rare, and almost entire lack of domi nance is not uncommon Evidently, then, dominance is not an essen tial feature of Mendelian heredity

Mendel's second law the law of segregation, or purity of gametes —While the body cells and the germ cells of the F_1 parent, prior to the reduction divisions involved in gamete formation, contain the determiners (genes) of both alternative characters and are therefore hybrid in character, a segregation of the alternative genes (allelo morphs) takes place during maturation so that only one or the other gene comes to be present in any gamete Thus gametes are pure for any gene A gamete has one or the other of a pair of allelomorphs and is never hybrid with reference to any single character This law is by far the most important of Mendel s discoveries In fact, it might be called *the* discovery of Mendel, for it is almost unsurpassed among biological generalizations on account of its far reaching applicability The law has sometimes been called the *law of the splitting of hybrids* Whether dominance is present or not, the law of segregation always holds The second law, therefore, is much more important than the first

Mendel's third law the law of independent assortment of differ-

ent allelomorphs —To use Mendel's own expression, "the relation of each pair of different characters in hybrid union is independent of the other differences in the two original parental stocks" This third law is only discoverable when we try to follow the assortment and recombination of at least two pairs of allelomorphs up to the second hybrid generation (F_2) If each allelomorph be studied by itself, it will show nothing more than the facts indicated in the first two laws, but as soon as we try to follow the modes of inheritance of more than one character simultaneously, we find that we are merely dealing with the independent shuffling and assorting of two or more genes The way in which we explain the third law is that all genes that exhibit independent assortment are located in different chromosomes If two allelomorphs were in the same chromosome, it is obvious that their association with each other in heredity would be much closer than if they were in different chromosomes Remember this when we come to consider a later proposition called *linkage*

Mendel's fourth law the law of recombination —According to Mendel, this law means ' that the constant characters which appear in the several varieties of a group of plants (or animals) may be obtained in all the associations which are possible according to the mathematical laws of combination " The genes carried by the chromosomes are shuffled about like a pack of cards and dealt out in all possible combinations according to the laws of chance The result of this is that the particular deal, or "hand," that happened to be possessed by the parent is likely not to be repeated in any of the offspring if the number of differences involved is at all large Of course, if there is only one point of difference between the two parents, the character of the parent will be repeated in one out of each four individuals of the F_2 generation If there are two pairs of allelomorphs concerned, there will be one in sixteen in the F_2 with the same combination as each original parent, if three pairs of allelomorphs, one in sixty-four, if four pairs, one in two hundred fifty six, if ten or more pairs, one in hundreds of thousands or millions Nearly all human beings differ from one another with regard to hundreds of allelomorphs Is it not remarkable, then, that there is as much resemblance between two brothers as there sometimes is? This condition will be better understood when we come to discuss the limitations of the law of independent assortment, which Mendel failed to discover, and which is explained by the law of linkage

The concepts expressed in the above laws may be considered to have originated with Mendel It must be remembered, however, that

Mendel had no knowledge of chromosomes or of the chromosomal mechanism of maturation which now seems to be the machine responsible for the regularities seen in the various Mendelian ratios and for segregation in general It is remarkable therefore that Mendel foresaw a mechanism within the genetic apparatus of plants that coincides in principle with that subsequently discovered Among the great discoveries that have resulted from the use of Mendelian methods and procedures are the factor hypothesis the chromosome theory of heredity and of sex determination linkage and crossing over and the finer details of the heredity machine

The presence and absence theory —In its original form the presence and absence theory implied that some gene was present in the dominant individual that was absent in the recessive It has been discovered however that this theory fails to hold especially in cases of multiple allelomorphs and probably does not hold at all As an example of multiple allelomorphs we may cite the various eye-color mutants of *Drosophila* (see page 294) A whole series of eye-color conditions ranging from red to white are all known to be the result of mutational changes in the same gene with red the wild type condition being dominant over any of the mutant conditions Now these various colors such as vermilion pink salmon cream etc are all recessive to red but dominant over white This shows that the gene for eye color is present in all these mutants but is merely modified in various ways or in varying degrees

The presence and absence hypothesis therefore might then be stated as follows There is some positive element present in the dominant gene that is absent in the recessive allelomorph which prevents the recessive gene from expressing itself In this form the theory is rather helpful and serves to rationalize the practice now universal of representing any dominant gene by a capital letter such as *A* and the recessive gene by the equivalent small letter *a*

The factor hypothesis —Mendel believed that for each character there was a determiner that each determiner produced a character unaided According to the factor hypothesis as we have seen such simple characters as colors in plants and animals depend upon the interaction of several genes which are called factors because they are not single causes but merely co operative agents It is now coming to be believed that each character of the organism is the product of the interacting of many possibly all of the genes in the organism but that some of the genes affect a given character more than do others

It remains to be discovered to what extent each character is the result of the interaction of all the genes When once we learn that a single character may depend upon the interaction of two or more independently inherited and segregating factors or genes, it becomes possible to understand all sorts of puzzling and apparently non Mendelian ratios The adoption of the factor hypothesis has justified itself over and over again, for it has been the instrument that has led to a really scientific genetics and has served to bring under one category all sorts of hereditary phenomena that had formerly been considered fundamentally different Thus there is now no further need for the three categories of heredity alternative, blending, and particulate All three are now seen to be phases of alternative, or Mendelian heredity Especially striking is the way in which the idea of *multiple factors* ("cumultative or 'duplicate factors of some authors) has served to rationalize and to bring into line with other Mendelian phenomena the data about the inheritance of quantitative characters Another service of the factor hypothesis comes out in connection with the discovery of *lethal factors* There is a large number of genes or factors whose presence in the homozygous condition (i e when a given factor is present in both gametes that unite to form a zygote) leaves the individual derived from such a zygote lacking in something essential for life All such individuals in any breeding experiment will fail to survive, and their absence will be noted when the ratios of the various combinations are worked out The failure of a certain expected combination to appear in the F_2 generation is attributed to the presence of a lethal factor in the stock It can readily be proven that many of the surviving individuals possess the lethal factor in a heterozygous condition, having one dose of the normal allelomorph along with the lethal factor These lethal factors can be identified and located as readily as characters that actually appear The subsidiary hypothesis of lethal factors has had a far reaching influence upon some of the most advanced phases of modern genetic practice

CHAPTER XXII

SEX LINKED HEREDITY

Up to this point we have been dealing with Mendelian experiments in which no more than one gene in any given chromosome was concerned The various Mendelian ratios, including the modified ratios presented in connection with the factor hypothesis depend upon each of the different allelomorphic factors involved being in a different pair of chromosomes If two or more genes were in the same chromosome, one would not expect them to follow the laws of random assortment and random recombination The study of sex linked heredity opened the way to the discovery that particular genes are in particular chromosomes, that they tend to remain together in heredity, but that genes in homologous chromosomes are frequently exchanged in a mutual fashion This discovery has led to a knowledge of linkage and crossing over, and to the discovery of the detailed architecture of the germ plasm

Nearly twenty years ago a peculiar kind of heredity, known as sex linked heredity, was discovered and explained by Morgan We had previously known of this kind of heredity in man, as in the case of color blindness, free bleeding, etc , but its mechanism was not even guessed at It had long been known that color blind individuals are almost invariably males, that such males marrying normal women never have any color blind offspring, but that their daughters when mated with normal men have some color blind sons, but never color blind daughters Thus color blindness shows a strong predilection for males, and is called a sex linked character Free bleeding night blindness, and several other human characters are known to be inherited in the same fashion

The mechanics of this form of heredity was worked out by Professor T H Morgan as the result of his work on the classic fruit fly *Drosophila melanogaster* In this valuable little insect the eyes are typically bright red In a stock of typical red eyed flies Morgan one day noted one white eyed male This had been born of typical red-eyed ancestry, so the white eye character in addition to being sex-linked was a *mutant*, appearing suddenly without any preliminary steps To test the heritability of this new character, the white eyed

male was mated to a normal red eyed female The offspring of this mating were all red eyed in appearance (phenotypically), but the females were obviously all genotypically hybrid red and white eyed, for when mated with normal red eyed males half of their sons were white eyed and half red eyed but all daughters were red eyed Subsequent experiments showed that half of the daughters were pure red eyed and half hybrid red and white eyed Now what sort of mechanism in the germ cells could account for this peculiar but very uniform type of hereditary behavior?

Professor Morgan explained the whole thing in a beautifully simple way by assuming that the gene of the sex linked character was situated in the X chromosome of the mutant male, for the male has but one X chromosome along with a Y chromosome (see Fig 53) In the reduction division of the germ cells of this individual two kinds of male gametes (spermatozoa) are formed in equal numbers, one carrying the X chromosome with the white eyed gene and the other the Y chromosomes Now whenever a female gamete (egg) of the normal red eyed female used as a mate is fertilized by a sperm with the X chromosome, an XX individual or female will result, and all of these females will get the white eye gene along with the X chromosome from their white eyed father But whenever an egg is fertilized by a sperm with the Y chromosome, a male will be produced and all of these will be red eyed because they get their X chromosome from their mothers Why are not these female offspring possessing the white eye factor white eyed? Because they have also inherited an X chromosome containing the red eyed factor from their mothers, and red eye is dominant over white eye These red and white-eyed hybrid daughters are now bred to normal red eyed males, whose X chromosome carries the red eye factor The females will produce two kinds of gametes in equal numbers, one with the X chromosome carrying the red eye gene, the other with the X chromosome carrying the white eye gene, while the male will produce two kinds of gametes, one with an X chromosome carrying the red eye gene and the other with only a Y-chromosome Each kind of male gamete will unite equally often with each kind of female gamete, and the result will be four kinds of zygotes in equal numbers one in which two red eyed X chromosomes come together and produce a pure red eyed female, one in which a red eyed and a white eyed X-chromosome come together and produce a hybrid female, one in which a red eyed X chromosome and a Y chromosome unite to produce a red eyed male -and finally, one in which a white eyed

X chromosome and a Y chromosome unite to produce a white eyed male. This is the detailed procedure followed by all sex linked characters of this sort and is shown diagrammatically in Figure 69

We have seen that white eyes seem to be purely a male character inasmuch as it does not seem to express itself in females even when present in the germ plasm. Why is this not just a secondary sexual character like the differences in size and shape of the body that characterize the two sexes? The answer to this query is that if we perform the proper breeding experiment it is possible to transfer the white eye character to the female. For example let us take one of the daughters of a white eyed male and mate her with a white eyed male. The female is a hybrid carrying the white eye gene in one of her X chromosomes and the red eye gene in the other X chromosome. She will produce equal numbers of gametes with the two eye color genes. The male will also have two kinds of gametes one with a white eye bearing X chromosome and one with a Y chromosome. Random pairing of the types of gametes of the two parents will produce four classes of individuals in equal numbers: one female with a red eyed X and a white eyed X (phenotypically red eyed), one female with two white eyed X chromosomes and therefore white eyed, one male with a red eyed X and therefore red eyed, and one male with a white eyed X and therefore white-eyed. It is clear then that the white eye character is not limited to one sex but merely closely linked to the male sex under normal breeding conditions. All sex linked characters are recessive, for were they dominant they would express themselves somatically when either one dose or two doses of the gene are present. The reason why the character appears normally in males only is that males have only one X chromosome, a situation which makes it possible for any recessive gene located in the X chromosome to express itself. The female, however, has always two X chromosomes and unless she inherits the recessive gene from both parents—a condition that would rarely occur in nature—she would always have the corresponding dominant character in one X-chromosome to mask or offset the recessive character in the other X chromosome. In man it is also the unfortunate male that falls heir to all of the rather detrimental sex linked characters, while the female, though inheriting the character more often than the male, practically never shows the effects of it.

An interesting variant upon the usual type of sex linked breeding experiment is the so-called *reciprocal cross*, starting out with a white

eyed female, derived from such an experiment as that just described, and breeding her to a normal red eyed male The F_1 hybrids will be white eyed males and red eyed females, the two eye colors simply changing sexes This is explained by the fact that females always inherit an X chromosome from both father and mother, while males always get their X chromosome from their mothers We speak of this

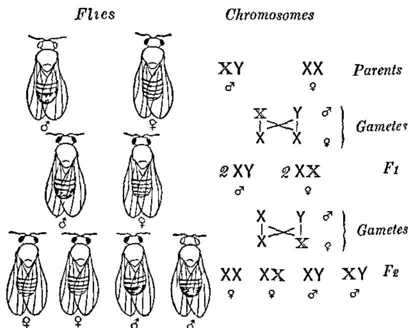


FIG 69 —Sex linked inheritance of white and red eyes in *Drosophila* Parents white-eyed male and red eyed female F_1 red-eyed males and females F_2 red eyed females and equal numbers of red-eyed and white-eyed males A black **X** indicates an X-chromosome bearing the gene for red eye a white X bears white eye **Y** is the Y-chromosome (*From Conklin, after Morgan*)

phenomenon as *crisscross inheritance* There are many evidences that, in general, daughters inherit more largely from fathers and sons from mothers, and it is probable that the mechanism of this condition is like that just described But to continue the reciprocal cross experiment to the F_2 generation, let us breed together the males and females of F_1 The result will be red eyed males and females in equal numbers (Fig 70)

The type of sex linkage which we have just described for *Dro*

sophila and which also prevails in man has come to be called the *Drosophila type* of sex linkage There is, however, quite a different type that is called the *poultry type*, which, while strikingly like the type already described differs from it in one important respect

The poultry type of sex linkage—In the *Drosophila type*, the female is the homozygous sex (producing only one kind of gamete, each

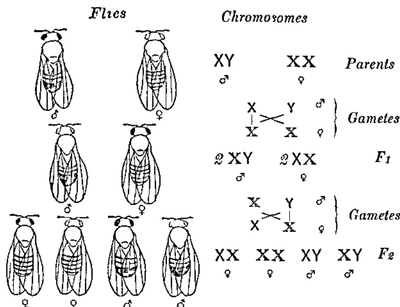


FIG 70—Reciprocal cross to that shown in Figure 69 Parents red-eyed male and white-eyed female F_1 white eyed males and red eyed females (criss cross inheritance —Morgan) F_2 equal numbers of red eyed and white-eyed individuals of both sexes The distribution of the sex chromosomes is shown at the right as in Figure 69 (*From Conklin after Morgan*)

with an X-chromosome) and the male is heterozygous (producing two kinds of gametes, one with an X and one with a Y chromosome) Now certainly in moths and butterflies, and probably in birds, the male is homozygous and the female heterozygous It is the custom to *designate the sex chromosome condition as WW for the male and WZ for the female*, though why we should not use XX and XY it is difficult to say With this reversal of sex chromosome composition of the two sexes we might expect that sex linked heredity would work out just

the reverse of that described for *Drosophila* so far as the sexes are concerned and this interestingly enough is exactly what we get

A typical instance of sex linkage of this sort is seen when a barred Plymouth Rock cock is mated with a Black Lanshan hen (Fig 71) All offspring both males and females of the F_1 generation are barred

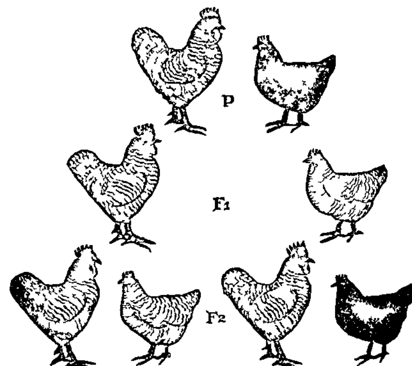


FIG 71 —Sex linked inheritance of barred and unbarred (black) plumage in poultry P parents barred male unbarred female F barred males and females F2 males all barred females in equal numbers barred and unbarred (*After Morgan*)

but when the individuals of F_1 are interbred (or the F_1 males are bred with any barred females) all males are barred and half of the females are barred and half are black Here we see that the recessive character black is linked with the *female* sex If we cross a black female with an F_1 male we can get equal numbers of barred and of black males and females The *reciprocal cross* (Fig 72) illustrates *crisscross* inheritance Starting with a black male and a barred female we get in F_1 barred males and black females When the F_1 individuals are interbred we get half barred and half black males and females

While in the birds the chromosomal condition has never been completely worked out, on account of inherent technical d[illegible] *likely to be overcome an*[illegible] has been thoroug[illegible] plan and the gam[illegible] *been found to be all alike* while

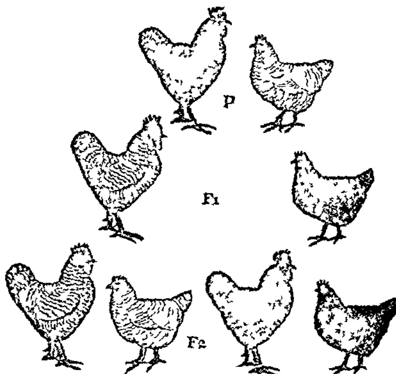


Fig 72 —Reciprocal cross to that *shown in Figure* 71 P parents unbarred *male* barred *female* F_1 barred males unbarred females (*crisscross inheritance*) F_2 barred and unbarred birds *equally* numerous in both sexes (*From Castle*)

those of the female are of two types one containing an X-chromosome (W-chromosome) and the other a Y-chromosome (Z-chromosome) The striking parallelism between the reversal in sex linked heredity and in the visible reversal of chromosome composition in these two groups of animals (*Drosophila* and man, on the *one* hand, and the *butterflies, moths, and birds, on the other*) offers one of *the* most cogent proofs of the validity of the chromosome theory of heredity, which we have already come to rely upon and shall have further occasion to make use of later on

To bring the facts of sex linked heredity sharply into focus by way of summary let us quote from D F Jones a genetic formulation of the whole matter

"*Rules for sex linked inheritance* —From this series of facts the following rules governing the transmission of sex linked characters can be deduced

"1 When the *homozygous* sex transmits the *dominant* factor, all of the offspring in the first generation exhibit the dominant character and the second generation is composed of three dominants to one recessive, the latter having the same sex as the recessive grandparent

"2 When the *homozygous* sex transmits the *recessive* factor, both dominant and recessive characters are exhibited in the first generation but exclusively upon the opposite sexes, and in the second generation both sexes show the sex linked characters in equal numbers"

CHAPTER XXIII

LINKAGE, CROSSING-OVER, AND THE ARCHITECTURE OF THE GERM PLASM

Owing to the fact that most of the important advances in our knowledge of the finer structure of the heredity machine have been made with the aid of the little fly *Drosophila melanogaster*, this chapter might be dedicated to the memory of this insect "Although like Cinderella, *Drosophila* comes from the humble environment of the garbage can,' says Walter, ' yet this fly has easily outstripped all its sister competitors for genetical honors, until today it stands probably as the most famous experimental organism in the whole world "

But too much credit for the genetic revelations derived from a study of *Drosophila* must not be given to the fly, which of its own accord would never have told us anything Though the name of *Drosophila* may now be famous all over the world, the one who made it famous is *Professor T H Morgan* who in collaboration with an unusually able corps of assistants (especially Sturtevant, Bridges, and Muller) has demonstrated to the scientific world the value of co-operation in research The old adage that two minds are better than one has proven true in this long and arduous, and above all fruitful, investigation The work done by "the fly squad,' as it has been affectionately called by fellow biologists, has resulted in an analysis of the heredity machine so detailed as to be almost unbelievable It seems too good to be true, yet the keenest critics of the work have failed to find any real flaws in the intricate fabric of conceptions that has been woven The whole story of this brilliant discovery, or series of discoveries, cannot be told in a way that would be intelligible to the layman or even to one with only a superficial knowledge of genetics It requires long and arduous study to understand it all, and one of the reasons why the ideas have failed of general acceptance is that only relatively few biologists have been willing to devote to the study of the data the amount of time and labor necessary fully to understand them

LINKAGE

In the last chapter a detailed account was given of the sex linked inheritance of white eyes in *Drosophila* This was the first of the sex

linked characters discovered in *Drosophila*, but by no means the last Soon after the discovery of the white eye mutant there appeared in typical stock characterized by gray wing color a single male mutant distinguished by yellow wing color, and this character was found to be inherited exactly after the manner of white eyes In other words, it is sex linked, and therefore must have its gene in the X chromosome As time went on, many new sex linked characters appeared as mutants always noted in males, and these characters had to do with all sorts of bodily characters Several of these were new eye colors (vermilion, ruby, prune, garnet) others had to do with eye shape or eye texture (furrowed, bar eye, and small eye) others with wing size and shape (broad wing club wing cut wing, vestigial wing), others, with bristles (scute, singed, forked) others with body color (tan, sable), and some were lethal characters Altogether over sixty definite sex linked mu tant genes, with their allelomorphs have been found to be sex linked and therefore must have their loci in the X chromosome

Now, during the twenty years of breeding millions and millions of *drosophilas* and examining them for signs of new hereditary char acters, some hundreds of other mutations were noted and their modes of heredity studied This latter great collection of mutant characters showed no sex linkage so could not be assigned to the X-chromosome They must in all probability be located in the *autosomes*, as the rest of the chromosomes are called But which of the remaining chromo somes carry the various non sex linked genes is not definitely known An important fact however, soon came to light, namely, that prac tically all of these non sex linked genes fall naturally into two groups of nearly equal size The basis for this distribution of genes into two groups is this that some of the characters appear together more often than not, while other characters appear apart (i e, in separate indi viduals) more often than together in the same individual This pro cess of classifying characters results in two large groups of characters of nearly equal size, each rather more numerous than the sex linked group The two large classes of genes that seem to hang together in heredity more often than they go apart have come to be assigned to chromosomes II and III (Fig 53) respectively, and are known as the *second and third linkage group* At present it is not possible to dis tinguish between Chromosome II and Chromosome III, for they are of the same size and shape, but the point is that there are only two other pairs of large chromosomes in *Drosophila* and only two large linkage groups besides the sex linked group What more natural,

then, than to assign these two large linkage groups to the two large chromosomes that are present?

All went well with the linkage hypothesis for awhile, but before long one of the workers discovered a new character that was not at all linked with any of the three groups and therefore could not be assigned to any chromosome known at that time This seemed at first like a staggering blow to the hypothesis then entertained, but it turned out to be one of the best demonstrations of its validity A re-examination was made of the germ cells of *Drosophila* with the result that a pair of tiny chromosomes was found to be always present, which because of their very small size, had been overlooked by the original students of this material This tiny chromosome was called Chromosome IV, and the new mutant, bent wing, was assigned to it Some time later another aberrant mutant, eyeless, was found that was closely linked with bent, and therefore assigned to Chromosome IV So far, these are the only genes that have been located in the tiny chromosome This may mean that there is not room for many genes in so small a body

Now, if there is anything in the chromosome theory of heredity and if the genes of individual differences have their seat in the chromosomes, all of the character differences in *Drosophila melanogaster*, no matter how many are found, must be in no more than four groups for there are only four kinds of chromosomes in that species For a while it was feared that some new character would appear that was not linked with any of the known linkage groups for the discovery of such a character would strike a severe blow against the theory of linkage and against the chromosome theory in general After the passage of several years, however, and the discovery of almost a hundred new mutants, not one has been found that does not show linkage with one of the four known groups Just to the extent that the finding of a fifth group of characters would have weakened the chromosome theory to that extent the failure to find any exceptions to the four linkage groups strengthens the theory

The characters represented by genes in both second and third chromosomes have to do with all parts of the body, including eye color, eye shape, body color, wing size and shape, bristle characters leg form, and lethal characters It cannot then be said that any one chromosome carries genes characteristic of any one part of the body, instead, it seems that every chromosome carries genes that affect every part of the body or, in other words, the whole organism

Confirmatory evidence of the validity of the theory of linkage comes from the comparative study of other species of *Drosophila*, some of which have the same number of chromosomes as has *D melanogaster*, others of which have a larger number In one species that has four pairs of chromosomes like the original species, only four linkage groups have been found, while in other species in which an extra pair of chromosomes has been found there is a fifth linkage group Comparative studies upon the linkage groups and the kinds of genes in these linkage groups have revealed a striking parallelism between the different species and a beautiful conformity between the numbers of chromosomes and the number of linkage groups Also it should be said that the relative numbers of genes discovered is in a rather definite proportion to the size of the chromosomes

CROSSING-OVER

All of our studies of the mechanism of heredity up till now have led to the conclusion that chromosomes are very definite and individual structures that continue from generation to generation intact and are passed as wholes from parent to offspring We have spoken of the process of pairing of homologous chromosomes in synapsis as though this pairing were no more intimate than a mere temporary embrace We have spoken as if, during the reduction division to form gametes the homologous chromosomes merely part company and proceed intact to opposite poles of the dividing cell and enter separate gametes unaffected by having associated in the embrace of synapsis That this is far from true has been revealed by an exact numerical study of the varying degrees of linkage in the characters whose genes are supposed to be located in a single member of a given chromosome pair On the basis that a chromosome is an inviolable body proceeding as a whole from generation to generation, we should, of course, expect any two characters that were once represented by genes in the same chromosome to stay together perfectly, i e , always to appear together in the same individual The fact that this result was not realized led to further advances in our understanding of the complex heredity machine Let us see just how linkage works out with certain genes in the X-chromosome Remember that each of the characters was located in the X-chromosome because each one by itself followed the mode of heredity of a sex linked character

The mode of linkage of two sex-linked genes—The wing color called "yellow" and the eye color called 'white have already been

dealt with in the previous chapter and were seen to be sex linked Now let us assume that by the proper breeding experiment we have a yellow winged white eyed female (call her yellow white for short) Mate her with an ordinary normal male with gray wing and red eyes (call him gray red) All the daughters are gray red like the father (each having inherited an X chromosome from him) but the sons are yellow white like the mother (having inherited her X chromosome) The Y-chromosome does not affect the result at all The daughters in addition to rece ving an X chromosome from the father receive another X chromosome from the mother so they have two different X chromosomes They are all phenotypically gray red because gray and red are dominant over yellow and wh te

Now it is easy to test the composition of these hybrid females by breeding them with double recessive (yellow white) males The result is as follows 49 5 per cent of offspring are yellow wh te 49 5 per cent are gray red 0 5 per cent are yellow red and 0 5 per cent are gray white Such a result as this could hardly be anticipated If there were no linkage but entirely independent assortment as would be the case were the two pairs of genes in different chromosomes we should expect the dihybrid ratio of nine gray reds three gray whites three yellow reds and one yellow white If on the other hand chromo omes reta n their integrity when they separate after synapsis we would expect 50 per cent gray reds and 50 per cent yellow whites Why do we find the anomalous ratios that we do? Obviously the chromosomes that pair in synaps s do not always part company without being affected by the chromosomal embrace but instead they seem

and in exactly the same number of cases the red and wh te genes are traded between chromosomes without the yellow and gray be ng traded along with them This mutual and perfectly equitable exchange of genes between homologous chromosomes is called *crossing over* and the percentage of crossing over between any two allelomorphs is the same each time the same breeding experiment is repeated under the same conditions In the case we have just described the crossing over percentage is very small only 1 per cent. Let us try another pa r of sex linked genes

A female with white eyes and miniature wings is bred to a male with red eyes and long (or normal) wings The miniature-wing gene

has already been shown to be sex linked The result in F_1 is that all females are red long and all males are white miniature Inbreed the individuals of F_1 and we get in F_2 33 5 per cent white miniatures, 33 5 per cent red longs, 16 5 per cent white longs, and 16 5 per cent red miniatures In other words, the crossing over percentage is 33 If the crossing over percentage were to equal or exceed 50 per cent, it would mean that there is no linkage at all, for if the two allelomorphic genes were in different pairs of chromosomes we should have even chances of two independent characters coming together or staying apart Thus we may say that in the first experiment the linkage (99 per cent) is very high and the crossover percentage is very low (1 per cent), while in the second experiment the linkage is relatively weak (67 per cent, or only 17 per cent stronger than no linkage at all) and the crossover percentage is relatively high (33 per cent)

The mechanism of crossing-over —' If it be admitted," say Morgan, Sturtevant, Muller, and Bridges, in their volume *The Mechanism of Mendelian Heredity*, that Mendelian factors are carried by chromosomes it can not be denied that interchange between homologous chromosomes must occur, for sex linked factors cross over from each other, and yet are known to be in the same pair of chromosomes since they all follow the X chromosome in its distribution The evidence allows no other interpretation But why should crossing over take place so rarely between certain factors and so often between others? We can make use here of certain information in regard to the chromosomes that gives a very simple answer to the question In the early germ cells, before the maturation period begins, the chromosomes appear to be scattered in the nuclei, and the homologous chromosomes in many cases show no tendency to lie together, although in some animals, *e g*, in many flies, the members of a pair are often found side by side In this early period the germ cells divide as do other cells and thereby increase in numbers But at the termination of this period, the homologous chromosomes unite in pairs There has been much controversy as to how this union takes place, but in some cases at least the uniting chromosomes twist around each other as they come together This is illustrated to the left in Figure 73 As a consequence, parts of one chromosome will come to lie now on one, now on the other side of the mate If when the twisted chromosomes separate, the parts on the same side go to the same pole the end result will be that shown to the right of Figure 73 Each chromosome has interchanged a part with its mate This process has been called crossing-over It is,

of course, also possible that the twisted chromosomes do not break and reunite where they cross, and if they do not, then when they begin to separate they simply pull apart irrespective of the side on which they lie. When this occurs each chromosome remains intact and no crossing over takes place.

'The chance that such a process of crossing over will occur between any two given points on the chromosome should obviously be greater the greater the distance between those points. If then the Mendelian factors lie along the chromosomes, the amount of crossing over be-

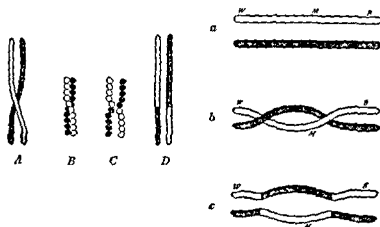


Fig. 73.—*B* and *C* illustrate Morgan's idea of the linear arrangement of the genes in the chromosomes. *A* and *D* show how the composition of the chromosomes is supposed to change as the result of the crossover. On the right a pair of chromosomes *a* before, *b* during, and *c* after a double crossover. (*After Morgan.*)

tween any two of them will depend upon their distance apart. Should two points lie near together a cross over will only rarely occur between them; if they lie farther apart the chance of such a cross-over taking place at *some point* between them will be greater. From this point of view the percentage of crossing over is an expression of the 'distance' of the factors from each other.

CHROMOSOME MAPS INDICATING THE ARRANGEMENT OF MENDELIAN FACTORS OR GENES IN THE CHROMOSOMES

By making use of the fertile idea explained in the last paragraph, that the percentage of crossing over between any two factors indicates their relative distances apart, it was possible to map out the rela

tive positions of all known factors The unit of distance on the map is that between two genes that have a crossover value of 1 per cent Haldane has proposed the term *morgan* for this unit of map distance These map units are only relative units, not absolute, as will be shown later The validity of the crossing-over hypothesis and of the chromosome maps may be tested in an almost infinite number of ways For example let us take a simple case of the so called three-point method of locating a new factor Suppose we have already determined the crossover percentage for two factors *A* and *B* to be 6 per cent A new factor *C*, appears which belongs to the same linkage group as *A* and *B*, and we wish to locate it First we work out its crossover percentage with *A*, and it turns out to be 4 per cent We then can predict that the crossover percentage between *B* and *C* must be either 6+4 (10) or 6 −4 (2) If, on working out the percentage, it coincides with the theoretical prediction, the method of locating genes in the chromosome receives strong support In practice, it may be said, the method works out perfectly for short sections of the map but breaks down somewhat for long map distances, for the reasons indicated below

Double crossing-over, an explanation of apparent discrepancies between map distances and crossover percentages —This matter is best explained by the use of a concrete instance Let us take three sex linked genes, white, miniature, and bar The crossover percentage observed between white and miniature, as has already been shown, is 33, that between miniature and bar is 22 The expected crossover percentage between white and bar is either 33+22 (55) or 33−22 (11), but the observed value is 44 per cent The proposed explanation of this apparently serious discrepancy is given by the authors of the theory as follows

"If we represent the percentages of crossing-over as relative distances along the chromosome the three points will lie as shown in Figure 73, *a* If crossing over takes place between white and miniature and between miniature and bar, then it might be expected sometimes to take place in both regions at once, as shown in Figure 73, *b* The result here would be to produce two chromosomes like those shown in the lower figure (Fig 73, *c*) The combinations of factors which these two chromosomes resulting from double crossing-over would contain, are white long bar and red miniature round Since these two classes of gametes are actually produced, the results of the experiment fulfill the theoretical expectation.

"There is a corollary of importance to this conclusion When a cross is made that involves only white and bar, the double crossing-over, that can be detected only when an intermediate point is followed, must still be supposed to take place Whenever it does take place white bar flies and red round flies result These will be added to the non-crossover classes since they have the same external characteristics Consequently, the non crossover classes will be increased and the crossover classes decreased In fact, the sum of the two crossover percentages 33 and 22 (55) is much greater than the apparent amount (44) of crossing-over when only bar and white are involved Here then we have an explanation of why long distances taken as a whole give too little crossing over, as compared with the same distances taken section by section The lowered percentage is an actual necessity owing to the occurrence of double crossing over"

Interference —One of the neatest confirmations of the crossover hypothesis is one that was first advanced by Muller According to this idea, whenever double crossing over occurs, two points of crossing-over cannot be near together unless the chromosomes coil rather tightly about each other Consequently, if crossing over occurs at a given point there cannot be further crossing over at the same time at nearby points Now it has been actually demonstrated that this is true, for genes in the neighborhood of a crossed over gene do not themselves cross-over with that gene in the degree expected on the basis of the law of probability This is supposed to be a sort of *interference* with free crossing over "It may be supposed," says Castle, "that chromosomes are somewhat like sticks of candy Break one in two at one point and it is unlikely that a break will occur simultaneously within a short distance of the first break, the strain there being already relieved" The fact that what must be expected in this case is actually realized in every case goes far toward establishing the validity of the whole crossing over hypothesis and the use of this hypothesis in showing the linear arrangement of the genes in the chromosomes

In this chapter it is hardly feasible to present any further evidence in support of the claims of the *Drosophila* school of geneticists that they have actually discovered the inmost secrets about the finer details of the mechanism of Mendelian heredity Suffice it to say that the evidence is voluminous and consistent. Not a single fact has come to light which is incompatible with the hypothesis, and new facts are continually coming to light that agree with the hypothesis and lend it

further support The opponents of the hypothesis are yearly becoming fewer and fewer, and the few remaining irreconcilables are having less and less to say It should be said, then, in all fairness that the hypotheses discussed in this chapter have been most fruitful in leading to new discoveries, and in last analysis this is the only fair test of a hypothesis If it is fruitful, it is good

The crowning feat of the *Drosophila* workers is the making of the chromosome maps of the species studied While it is impossible to obtain the latest version of the map, for the reason that new loci are continually being added the accompanying map (Fig 74) gives the locations of the genes that have been determined most carefully It will be noted that not only have the genes in the X chromosome been located, but also those in the other three chromosome pairs A few additional situations that have arisen out of the studies involved in making the map will now be discussed, and then this somewhat difficult chapter will be brought to a close

Multiple allelomorphs —In a previous connection we have discussed the multiple factor hypothesis as an explanation of quantitative heredity Multiple factors are duplicate factors located in different chromosomes Quite definitely in contrast with that situation is one in which different factors or different forms of the same factors occupy the same locus of the same chromosome For example, red eye in *Drosophila* is a single factor A change in the red-eye factor gives white eye, another change in red gives cherry, another gives eosin, and several other definite mutant colors resulting from changes in red have been observed Now each of these changed color factors is an allelomorph of red and each is also an allelomorph of any of the others By this we mean that, if a cross is made between individuals differing with respect to any two of these alternative colors of eye, one will be dominant over the other in the F_1 generation, and there will be three dominants to one recessive in the F_2 generation One of the assumptions about allelomorphic genes is that they occupy equivalent locations in homologous chromosomes This can be put to a crucial test No more than two members of a set of multiple allelomorphs can be present in one individual because there are only two homologous chromosomes and hence only two equivalent gene loci This proves to be true, for when red eye and white eye enter into a cross only these two eye colors come out of it, when cherry and white go in, only cherry and white come out, when red and cherry go in, only red and cherry *come out Several other authors have found interesting sets of multi*

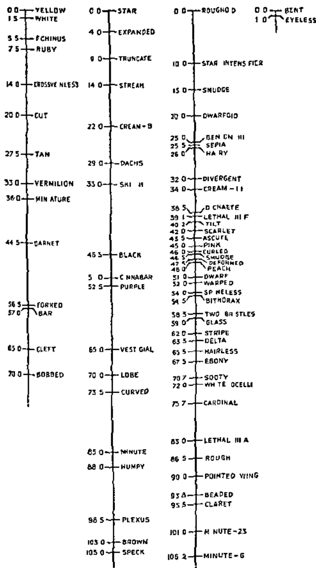


FIG 74 —The chromosome map of *Drosophila melanogaster* (*After Morgan and Bridges*)

ple allelomorphs in other animals Nabours, for example has described a very interesting series of these for the grasshopper, *Hes perotettix*, Sewall Wright has described a considerable number of such cases in guinea pigs and Bellamy has worked out an explanation of a very intricate piece of hereditary behavior in fish hybrids that involves the use of the multiple allelomorph scheme

Lethal factors again —A study of the chromosome map of *Drosophila melanogaster* will show that many of the located factors are *lethal* This perhaps needs further explanation Many of the factors that we have previously dealt with in this insect are more or less unimportant to the life of the animal Such things as slight changes in eye color, body color, bristle arrangement, etc , are not very important, nor do they affect the viability of their possessors Some factors, on the contrary, have been found to be so essential to the life of the individual that their absence causes death The loss of or detrimental change in a vital character is known as a lethal factor Of course all such factors are recessive, otherwise they never could be inherited As it is, an individual may have a lethal factor in the heterozygous condition, balanced by the normal dominant character When, however, two such heterozygous individuals breed together, one fourth of their offspring, according to the simple Mendelian rule, will get the lethal factor from both parents These homozygous recessive lethal zygotes cannot live so the ratio that actually appears is one homozygous normal to two heterozygous individuals (phenotypically normal), and that is all One of the best known cases of this kind of hereditary behavior occurs in mice Yellow mice when mated together give one gray to two yellows The production of grays from yellows shows that the yellows were heterozygous, or hybrid yellow and gray It is noted that the litters of these mice average one fourth smaller than other mice What becomes of the lost one-fourth? An examination of the uteri of yellow mice reveals a number of dead embryos equal to the expected ratio of pure dominant yellows These constitute the missing class and prove the presence in yellow mice of the recessive lethal factor associated with the yellow factor

LINKAGE IN OTHER ORGANISMS

Lest the reader leave this chapter with the impression that linkage is a phenomenon confined to flies and mice, we shall close this chapter with the table on the next page taken from Castle, which shows how widespread is the occurrence of linkage and crossing-over in both the

CASES OF LINKAGE IN PLANTS OR IN ANIMALS OTHER THAN DROSOPHILA

Species	Group	Linked Characters	Cross-over Percentage	Linkage Strength	Authority
Sweet pea	1	Purple flowers, long pollen	11 or 12	76–78	Bateson and Punnett
	1	Purple flowers, erect standard	0.78	98.4	
	1	Long pollen, erect standard	12.5	75	
	2	Dark axil, fertile anthers	6.2	87.6	
	2	Dark axil, normal (not cretin) flower	?		
	2	Fertile anthers, normal (not cretin) flowers	25.0	50	
Primula sinensis	1	Short style, magenta corolla	34.0	32	Altenburg
	1	Short style, green stigma	40.6	18.8	
	1	Magenta corolla, green stigma	11.6	76.8	
	1	Tinged corolla, green stigma	?		Gregory
	1	Pale stem, green stigma	?		
Garden pea	1	Round seeds, tendrils on leaves	1.5	97	Bateson and Vilmorin
	2	Late flowering, colored flowers	12.16	68–76	Hoshino
Antirrhinum	1	Red flower color, "picturatum" pattern	20.0	60	Baur
Maize	1	Waxy endosperm, Aleurone C	26.7	46.6	Breggar
	2	Aleurone R, Chlorophyl G	19.0	62?	Lindstrom
	2	Aleurone R, Chlorophyl L	0.0	100	
	2	Chlorophyl G, Chlorophyl L	23.0	54	
	3	Starchy endosperm, tunicate seed	8.3	83.4	Jones
Tomato	1	Vine habit, fruit shape	20.0	60	Jones
	2	Green foliage, 2 celled fruit	0?	100?	
Beans	1	Seed pattern, vine habit	0?	100?	Surface
Silkworm	1	Pattern Q of larva, yellow silk	26.1	47.8	Tanaka
Apotettix	1	Patterns G and M	4 (in♀)	92	Nabours
	1	Patterns M and K	1 (in♀)	98	
	1	Patterns K and Y	6 (in♀)	88	
	1	Patterns Y and R	10 (in♀)	80	
	1	Patterns Y and T	12 (in♀)	76	
	1	Patterns R and T	0 (in♀)	100	
	1	Patterns M and R	10 (in♀)	80	
	1	Patterns Y and Z	10 (in♀)	80	
Pigeon	1	Sex linked factors I and A	40 (in♂)	20	Cole and Kelley
Rat	1	Albinism red-eye	1.0?	98?	Castle and Dunn
	1	Albinism pink-eye	21.0	58	
	1	Red eye, pink eye	18.3	63.4	
Mouse	1	Albinism, pink-eye	14.3	71.4	Castle and Dunn

animal and the plant kingdom In all probability it is a universal phenomenon, and if so, takes place in man There are, in fact, strong indications in man that fair hair and blue eyes are linked, but they show also considerable crossing-over Similarly, red hair and a certain type of disposition are popularly supposed to be linked, but crossing over may be a saving grace in this as in other cases

With this chapter we have arrived at the climax of discovery in the field of the mechanism of heredity This is undoubtedly the most intricate consideration dealt with in this volume In its very nature it is relatively difficult to understand We have tried to explain everything in a decidedly circumstantial way, and it is hoped that some success in an endeavor to attain clearness has been attained

CHAPTER XXIV

CROSS BREEDING AND INBREEDING

Cross breeding is essentially the same as hybridization, and we have already studied various phases of hybridization in connection with Mendelian heredity There are, however, certain other aspects of cross breeding that have only a more or less remote connection with Mendelian analysis

The rôle of hybridization in evolution —"This," says R R Gates "is a thorny subject, on which different investigators have taken quite different attitudes to the same facts The extreme view that all flowering plants, or even all sexual organisms, are hybrids has been held This has been accompanied in some cases (Lotsy) by the denial of any true germinal change, though why such labile substance as protoplasm should be incapable of undergoing a permanent or germinal change is difficult to understand Jeffries and others appear to hold that polyploidy and other changes in which hybridization may be a factor, have nothing to do with evolution A more reasonable view would appear to be that crossing has occurred in various groups from time to time, with more or less frequency and between sometimes more and sometimes less closely related forms Crossing is therefore a condition under which much evolution has taken place It by no means follows that crossing any more than gravitation is a *vera causa*, still less *the vera causa*, of evolution, but it is a contributing condition Polyploidy, frequently accompanied by hybridization, appears to be a common occurrence among flowering plants, but it would be futile to deny on this account that flowering plants have had an evolution, nor would it be safe to assume at present that the evolution of this group differs very essentially from that of any other"

The exact rôle of hybridization in the formation of new species is at present merely a matter for speculation but that many new races have been the result of favorable combinations of the genetic factors of different strains can scarcely be doubted In a sense, it may be said that hybridization is the rule in all organisms that reproduce sexually, for no completely homozygous individuals exist in such groups, and therefore there will always be a certain amount of factor segregation in gamete formation and of recombination in the process of zygote formation Also, it must be admitted that there are all grades of hetero

zygosity within a species and between one species and another Moreover, sexual reproduction as an adaptation operates chiefly through bringing together a variety of combinations of characters possessed by strains genetically diverse, it is, in fact, a hybridizing mechanism It seems probable therefore that hybridization as a factor in evolution operates up to the limit of the adaptive possibilities inherent in its mechanism We may therefore conclude that hybridization is and has been an important evolutionary factor, though we have at present little information as to its precise mode of operation as an agent in species formation

SOME ANIMAL HYBRIDS

One of the arguments offered by the advocates of the theory that hybridization has played a prominent part in species forming in nature is that man has carried on so much successful hybridization between different species of animals and plants and has produced many very useful hybrids, some of them better adapted than either of the parent types from which the hybrids were derived

Especially interesting are animal hybrids produced by interbreeding distinct species of domestic and wild animals Our brief account will be confined to horse, cattle, and fowl hybrids

Horse hybrids —These hybrids are all the product of crossing different species of the genus *Equus* The commonest hybrid is that between the mare of the horse proper, *Equus caballus*, and the jack of the species *E hemionus* The result is the mule, a useful domestic animal combining some of the best features of the two species and superior to either in vigor, hardiness, capacity for work, and resistance to disease The reciprocal cross, made by mating a jennet to a stallion, is called a "hinny," a sort of small mule Neither mules nor hinnies are, as a rule, fertile, so they are not self perpetuating The rare reports of female mules giving birth to foals, when bred to jacks, are as yet not fully authenticated There is some possibility that the particular females in question were either rather large jennets, which of course would be fertile, or rather mulelike mares

The sterility of mules has been shown by Wodsedalek to be due to differences in the numbers of chromosomes in the two species, the horse having in the female 18 autosomes and 2 X chromosomes, the male 18 autosomes and one X-chromosome, the ass having in the female 32 autosomes and 2 X chromosomes, the male 32 autosomes and (according to Paynter) an X- and a Y-chromosome With this great discrepancy in chromosomes, it is hardly to be expected that meiosis could operate so as to give any sort of viable gametes or zygotes

A number of other *Equus* hybrids have been produced The horse has been crossed with the now extinct quagga (*E quagga*) and with several species of zebras And the zebras have been crossed with asses No particular use has been made of such hybrids

Cattle hybrids —There are many species of the genus *Bos* The auroch is designated *Bos taurus primegenus* The now extinct wild ox of Europe, supposed to be the ancestor of European cattle, is called *Bos taurus* The characteristic humped cattle of India is known as *Bos indicus* The wild ox of Java is called *Bibos sondaicus*, and hence belongs to a different genus The bison of Europe and the closely related American bison are called, respectively, *Bison bonasus* and *Bison bison* There are three species of buffalos belonging to the genus *Bubalus* Various hybrids, both interspecific and intergeneric have been made by crossing these and other species of cattle like animals Hybridization of European and Brahman cattle or zebus (*Bos indicus*), has been carried on very successfully in the southern states, especially in Texas and Louisiana The hybrids are vigorous, and both sexes are fertile The F_1 hybrids are predominantly of the European breed, with only the suggestion of the zebu hump and much less of the hang ing dewlap than in pure zebus When the F_1 individuals are interbred, there is a great deal of variation among the F_2 offspring, of which no satisfactory analysis has yet been made The chief advantage derived from introducing the zebu strain into American cattle is that zebus are immune to Texas fever, and hybrids with as low as one-eighth zebu blood are also immune to this most serious of cattle diseases

Bisons and European cattle have been successfully crossed, the cross usually made being between cattle cows and bison bulls The cross is successful only in a small percentage of cases and very fre quently both dam and calf are lost The sex ratio of these hybrids is very unequal, the ratio being at one time 33 females to 6 males Usually the F_1 males are sterile, but the females are fertile and may be back-crossed to bison bulls or cattle bulls as desired, and there is no difficulty or danger of loss of life as in the F_1 cross Animals that are the product of various grades of admixture of bison and cattle are called *cattalos* It is expected that, by selection, a desirable hybrid type may be fixed, combining the best features of both genera

Fowl hybrids.—The domestic fowl is commonly designated *Gallus domesticus* and is believed to have been derived from one or more of several wild species of the genus *Gallus* Four wild species are recog nized *G gallus*, the red jungle fowl of northern India, Malay states,

and Sumatra, *G lafayette* the Ceylon jungle fowl *G sonnerate*, the gray jungle fowl of southern India, and *G varius*, the jungle fowl of Java These birds are rather wild and do not hybridize well in captivity Yet occasional uncontrolled hybrids have been produced which are of interest in throwing some light on the origin of the various domestic breeds Darwin was of the opinion that all the domestic breeds have been derived from *G gallus*, for sometimes in India cocks of *G gallus* invade flocks of domestic fowls and mate with the hens, producing fully fertile offspring The same has been claimed since Darwin wrote, for the other species and some authors are inclined to believe that domestic fowls of different breeds may have been derived from different wild species of *Gallus* The evidence for the latter view, however is less abundant than for Darwin's contention

SECONDARY EFFECTS OF CROSS BREEDING AND INBREEDING

A. CROSS BREEDING

Hybrid vigor (heterosis) —It has long been known that the crossing of different races, varieties, or even species of animals or plants result in the production of first generation hybrids characterized by a greater sturdiness, vitality, and size than either parent species This effect has received the name *hybrid vigor* or *heterosis* A good example of this effect is the common mule, which is large and strong, thrives under adverse conditions, and is hardier than either parent It has the disadvantage, or possibly advantage, of being sterile, a fact which makes it necessary to hybridize two species every time we want another mule.

Some of the manifestations of hybrid vigor as observed in various crosses are as follows

a) Hastening of maturity —This is particularly advantageous in plants reared in regions where the growing period is short Thus hybrid strains of cereals may be valuable because they can be harvested sooner than pure-bred strains It is also true that hybrid plants, such for example as tomatoes, have a larger as well as an earlier yield.

b) Increased longevity —Pearl has shown that hybrid strains of fruit flies have a longer average life-span than pure races The same is true for a number of hybrid races of plants, as brought out by Gaertner

c) Better viability —The writer has shown that the hybrids produced by crossing the eggs of the fish *Fundulus heteroclitus* with the sperm of *F majalis* were frequently more viable, faster growing, and more vigorous than the pure-bred young of either species, but the hybrids from the reciprocal cross showed much reduced viability

Similarly, he has shown that some of the hybrids produced by crossing the eggs of the sea urchin *Strongylocentrotus purpuratus* with the sperm of *S franciscanus* lived nearly twice as long under cultural conditions as did either pure breed, while the reciprocal cross showed very low viability

d) Augmented facility of vegetative propagation —Many hybrid plants are noted for their success in vegetative propagation It is believed that plants such as strawberries, brambles, grasses, etc , that propagate so successfully by vegetative methods, are the products of hybridization The vegetative method of reproduction not only maintains a fortunate combination of genetic characters that could hardly be repeated by gametic reproduction but maintains their hybrid vigor as well

These and perhaps some other effects, all of which are essentially beneficial, have been noted in both animals and plants The following explanation of hybrid vigor has been given by D F Jones

"*Explanation of hybrid vigor* —From the illustrations given it is evident that there is a tendency for the features of both parents to be expressed in the offspring This is the basis for an understanding of the vigor derived from crossing There is a greater number of different hereditary factors in a hybrid individual than in either pure parent Nearly all variations that are recessive are less favorable to the development of the organism than their dominant mates Since crossing brings out those qualities which help the individual in its growth and suppresses the abnormal and unfavorable characters, it is to be expected that hybrids will tend to be strong and vigorous This will be true, however, only if each parent is able to supply the deficiency of the other and if the forms crossed are not so diverse that their union is incompatible with normal growth If the parents are themselves hybrids, further crossing may bring together no great number of dominant favorable growth factors but may even uncover recessive characters Hence further crossing can not usually increase size and vigor, and in fact may even result in the appearance of weaknesses This is clearly understandable from the operation of Mendel s principles of heredity "

The question now arises as to whether hybridization in general is advantageous or the reverse Undoubtedly first generation hybrids are generally an improvement upon either parent race, especially if the parents belong to races not too distantly related If we could stop hybridization after one generation, as Nature stops it in the case of the

mule, nothing but good would apparently come out of it, but in man and among other animals and plants where mating is more or less indiscriminate, cross breeding is sure to continue into the F_2, F_3, and subsequent generations, entailing the production of all sorts of unfortunate combinations and the outcropping of all sorts of unbalanced recessive weaknesses In view of these considerations it is practically certain that hybridization, unless accompanied by rigid selection and the elimination from parentage of the less desirable combinations, is on the whole disadvantageous In nature, natural selection serves to eliminate sooner or later the worst combinations resulting from continuous cross-breeding, but in man, little is done to prevent the worst racial admixtures from predominating, the result being that the populations of some parts of the New World are made up mainly of a rather homogeneous hybrid type possessing little more than the worst traits of the various races that have contributed to the melting pot

By way of a general summary let us quote the following paragraphs from D F Jones,[1] by whose book *Genetics in Plant and Animal Improvement* this discussion has been largely suggested

"*Summary*—From the foregoing it will be realized that if any individual is deficient or handicapped in its hereditary make-up, there is a good chance that its needs will be supplied when it is crossed with other individuals, because all are not apt to be wanting in the same things What one lacks is furnished by the other, and conversely, In other words, there is a pooling of hereditary resources, with the result that the combined effect is better than either could produce alone

"It should now be clear that the beneficial effects of crossing follow from the workings of the laws of heredity and not from any mysterious stimulus from the act of crossing itself If good qualities exist in the parents, but not in sufficient amount or not in their proper association, then there is a good opportunity for the offspring to bring together the favorable factors from both and surpass their parents in development This is a temporary and transitory effect, however The increased vigor is shown at its best only in the first generation following the cross, and is quickly lost in later generations unless it can be perpetuated by some form of asexual reproduction"

B. INBREEDING

There is a widespread and deep-seated feeling among men that the mating of close relatives is unnatural and harmful In most civilized countries there are laws both religious and civic forbidding the mar

[1] *Loc cit*

riage of close relatives The aversion to the marriage of relatives has sometimes gone beyond the limits of genetic relationship and has invaded the realm of merely legal or conventional relationships as in England, where it is, or at least once was illegal to marry one s deceased wife s sister

"Only exceptionally, as in the case of the royal families of Egypt and ancient Peru,' says Castle, "has the marriage of brother and sister been sanctioned The underlying reason in such cases was the belief that the family in question constituted a superior race whose members could find no fit mates outside their own number There was probably no thought that inbreeding itself was beneficial but only the desire to conserve the superior excellence believed to reside in certain individuals The same considerations probably have led to the occasional practice of inbreeding in animal husbandry, viz , the desire to conserve and perpetuate the superiority of particular individuals

It appears that Robert Bakewell, a stock breeder of the eighteenth century, was the first to show the value of close inbreeding in maintaining a uniform type of sheep and cattle Bakewell adopted the plan of mating brother with sister or parent with offspring, much to the horror of his neighbors, who considered such a procedure immoral, but their scruples were soon broken down by the obvious improvements obtained and the greatly increased revenue that accrued The practice of inbreeding has been a favorite one for a long time, and many fine breeds of standard character have been produced mainly in this way

Opinions among breeders differ as to whether inbreeding if practiced expertly is injurious Some believe that inbreeding itself involves no possible injury, others hold that it is always more or less harmful In order to settle this question geneticists have carried out extensive experiments under conditions of rigid control. Even these do not agree in their results One group of workers (Crampe and Ritzema Bos) found after extensive inbreeding of rats that there was a steady falling off in fertility and general health during the first six generations of inbreeding The material used, however, was a mixed or hybrid stock to start with, a fact that makes a satisfactory conclusion difficult. Weismann inbred a race of white mice for twenty nine generations In the first ten generations the average number of young was 6 1, in the second ten generations it was 5 6, and in the last nine generations it was 4 2 Again, nothing was known about the genetic constitution of the original parents

Recent experiments carried out by Dr Helen Dean King at the

Wistar Institute are entirely contrary to those of the workers just mentioned This piece of work was carried out in a most precise manner with large numbers of individuals The original stock consisted of four rather undersized but otherwise normal albino Norway rats Brothers and sisters were mated throughout the experiment For six generations no selective mating was practiced with the result that many of the defects previously noted were in evidence but after the sixth generation some twenty females from about a thousand were selected for their superior qualities From this stock the result of inbreeding for twenty five generations was very good Dr King seems to have produced an essentially homozygous race of white rats that are superior in many ways to the race from which they have been derived. It seems probable that selection has rid the race of all or nearly all of the residual recessive characters so that the present combination is highly normal and standard Sewall Wright under the auspices of the United States Department of Agriculture, has carried out a very extensive program of inbreeding with guinea pigs His results are more in harmony with those of earlier workers than with those of Dr King In general the result of brother and sister mating was a steady loss of vigor both bodily and reproductive Both prenatal and postnatal mortality was increased Some families however remained quite strong after long inbreeding while other families declined so rapidly that it was impossible to perpetuate them after a few generations Some strange combinations of traits appeared in different stocks One stock was characterized by very low vitality, but remained normal in body size and in number of young produced Another stock showed undiminished vitality but greatly lowered reproductivity and reduced size The chief difference in method used in these two modern experiments seems to be that only the best were bred in Dr King s experiments while in Dr Wright s exper ments no such precautions were taken probably because he preferred to approximate natural conditions

A large amount of experimentation in inbreeding has been carried out with domestic animals and plants of all sorts, and the results have shown as much diversity as those already reported consequently opinions are still at variance as to the question whether inbreeding is injurious per se D F Jones who seems to have given this matter very careful consideration takes the position that '*the only injury that comes from inbreeding comes from the inheritance received*' If the individuals inbred possess many undesirable recessive characters, nothing

is surer than that inbreeding will bring these to the surface Cross breeding might succeed in masking such recessive characters, but they remain in the germ plasm, nevertheless All inbreeding does is to reveal that which was masked behind dominant characters. Therefore it is not inbreeding itself that is to blame, but a poor heredity In breeding is a valuable instrument for detecting the unfavorable hereditary characters in a race and giving the breeder a chance to cull out the defective factors from his stock

Inbreeding should be followed by cross-breeding inbred stocks — Whatever loss of vigor or productiveness may be incidental to the in breeding method of standardizing stock may be entirely done away with by suitable cross breeding or outbreeding No matter how good an inbred stock may be, great improvement can be brought about by introducing new blood even from an apparently very similar strain which is unrelated It is well known that when two pure breeds are crossed there is an effect quite equivalent to that which we have called hybrid vigor The animal breeder commonly practices close inbreeding in building up families of superior excellence, which he maintains as pure-line stock, used for crossing with other stocks in order to produce exceptional F_1 offspring Man, of course, cannot practice this scheme in the present state of society, but it seems obvious that there lie in this method almost untold possibilities for racial improvement

CHAPTER XXV

CHANGE FACTORS INTRODUCTION

Change has already been contrasted with diversity by citing the analogy of the kaleidoscope (p 187) Another analogy may help to emphasize this difference If one were to shuffle and deal a very elaborate deck of cards, the hands dealt would show very great diversity, but there would be a certain statistical limitation to the number of possible combinations of cards After a time the whole series of possible combinations would be dealt out and the series would go on repeating itself and nothing new would appear so long as the cards remained unchanged Add a new card or a new series of cards, or merely change some of the spots on a card, and at once the whole character of the combinations produced would be altered Dealing an unchanged deck of cards is the sort of thing that the diversity mechanism (sex) does, but the mutation mechanism actually adds new cards or alters the spots Changes in the germinal substances themselves are called *mutations* Hence mutation is *the* change mechanism

CHANGING VIEWS AS TO THE ORIGIN OF NEW HEREDITARY CHARACTERS

Lamarck believed that all evolutionary change was initiated in the body (soma) directly or indirectly in response to environmental stimuli, causing increased or decreased functioning of parts He had no theory as to how such changes could be inherited, but assumed that they were This belief is embodied in his theory of the inheritance of acquired characters, known as the "Lamarckian theory"

Charles Darwin also believed that all variations that are frequent enough to serve as the raw material for selection originated in the soma in response to differences in the environment or indirectly, to changes in the amount of use to which a given part was put To account for such changes being hereditary, he proposed a theory with which he was not very well satisfied, for he called it "the provisional theory of pangenesis" According to this view, each part of the organism is continually giving off into the blood stream minute particles, "pangenes," each of which is characteristic of the particular status of a part of the organism at the time when the pangene was given off Thus a strengthened muscle or a more efficient eye, each resulting from in

creased functioning, would give off pangenes reflecting muscle or eye improvements Similarly, a deteriorating organ or tissue or even a damaged or diseased part would produce pangenes reflecting their condition Now these pangenes were believed to be collected in the gonads to form germ cells a germ cell being a concentrated mass of all the kinds of pangenes of the organism In this simple way somatic changes were believed to be inherited But the difficulty with this theory is that no such mechanism exists

Weismann was the first biologist to depart from the idea that hereditary changes originate in the soma He proposed the theory of the continuity and apartness of the germ plasm, and its corollary that all hereditary changes arise directly in the germ plasm His picture of the method of germinal change is expressed in his theory of 'germinal selection "

The essential feature of germinal selection, as the name implies, is a transfer of the struggle for existence to the germ cell The germ cell is assumed to be a greatly reduced and simplified sample of the characters of the whole organism Each independently variable part of the organism is supposed to be represented in the germ cell by a minute physiological unit, unique in composition and capable of reproducing the part in question in a new organism These hereditary units are called "determinants" Thus there is a different kind of determinant for each muscle of the body, for each bone, or for each independently functioning blood vessel, but, since all red blood corpuscles are alike, there would be only one determinant for all of them These determinants have to grow, and in cell division to divide so as to furnish to daughter germ cells all of the necessary determinants for a whole individual In their process of growth and multiplication which goes on very rapidly at certain periods in the germ cell cycle these determinants are in competition among themselves for the available food supply Some may be more favorably placed than others or may be more active chemically than others There will thus arise a struggle within the germ for a chance to grow and reproduce their kind, which, for these determinants, might be as bitter as would be the struggle in nature among the whole organisms that are in competition for a place in the world A determinant favored perhaps accidentally or possibly because of inherent activity, by a good food supply would wax stronger and grow faster and would, logically, produce a larger and more effective part when that particular germ cell developed into an adult Other germ cells that would be the offspring

of this germ cell would continue the struggle among determinants, and it would be expected that the strong determinant would continue to gain further advantage until the structure it represents reached its maximum efficiency Similarly, a determinant that was for some reason deprived of its fair share of nutriment at any time would be weakened and would produce in cell division weakened daughter determinants These in turn unless especially favored, would wage a losing fight and continue to grow smaller and weaker Each individual that might develop from such germ cells would have the characters whose determinant had been weakened in a reduced and progressively degenerating condition Finally, certain determinants might starve entirely, and the part for which they stood would disappear entirely from the ontogeny of the individual arising from these germ cells

In this way Weismann tried to explain the gradual dwindling and the final elimination of useless organs So also he would explain definitely directed or orthogenetic variations, because germinal selection, once started in a given direction, continues automatically till the goal of adaptiveness is reached

The most potent objections to the theory of germinal selection are as follows

1 There should be, according to this theory, certain pronounced tendencies in variability in definite directions, whereas fluctuating variations nearly always distribute themselves evenly about the mean or mode, and the same specific mean or mode is stationary in successive generations

2 The theory implies too rapid and too general modification of parts and therefore does not accord with the fact that species are decidedly constant, except for occasional mutations over long periods of time To meet this objection Weismann proposes a new self correcting mechanism that checks too rapid a development of characters.

3 The over or undernourishment of determinants might conceivably induce size changes in characters already present but could hardly be responsible for the origin of qualitatively different characters

4 Actual experiments in over and underfeeding of animals have been carried on by certain experimenters in order to test out the theory of germinal selection In the experiments of Kellogg for example involving feeding silkworm larvae only one eighth of the normal amount of food the only result was that the mature individuals were

dwarfed in size The relative sizes of the parts were unaltered showing that there had been no real struggle among the determinants for on the theory of germinal selection only the stronger determinants would have survived and the weaker ones would have been starved out. Partial individuals moreover, lacking certain organs and over developed in others would have been produced instead of individuals merely smaller in all parts

These are the specific objections to the theory, but more important than all of these is the general objection that follows

Thus Weismann says Morgan[1] ' has piled up one hypothesis on another as though he could save the integrity of the theory of natural selection by adding new speculative matter to it The most unfortunate feature is that the new speculation is skilfully removed from the field of verification and invisible germs whose sole functions are those which Weismann s imagination bestows on them are brought forward as though they could supply the deficiencies of Darwin s theory This is indeed the old method of the philosophizers of nature An imaginary system has been invented which attempts to explain all difficulties and if it fails then new inventions are to be thought of Thus we see where the theory of selection of fluctuating germs has led one of the most widely known disciples of the Darwinian theory

' The worst feature of the situation is not so much that Weismann has advanced new hypotheses unsupported by experimental evidence, but that the speculation is of such a kind that it is from its very nature unverifiable and therefore useless Weismann is mistaken when he assumes that many zoologists object to his methods because they are largely speculative The real reason is that the speculation is so often of a kind that cannot be tested by observation and experiment.

It seems almost impossible that the same Professor Morgan who wrote the foregoing paragraphs in 1903 should now be the leading exponent of a theory of the mechanics of hereditary transmission which depends upon hereditary units almost identical with Weismann s determinants for the genes or factors of Morgan are minute corporeal bodies in the germ cells which determine the characters of the adult individual

The difference is however that the genes of Morgan are experimentally demonstrable and have behind them a vast amount of real evidence for their existence

[1] From T H Morgan *Evolution and Adaptation*

MUTATIONS

Mutations are, by definition, changes in the germinal substance They may affect individual genes or whole bundles of genes (chromosomes) They may occur in the germ track or in the soma If they occur in the soma, the resulting change is seen in a local patch of changed cells the size of which depends on whether the mutation occurred early or late in ontogeny Since body cells do not produce germ cells, somatic mutations are no more heritable than are functional changes in the soma The only mutations of significance for evolution are those that occur in the germ track The various kinds of germinal mutations will be discussed at some length in the following chapter

CHAPTER XXVI

THE MUTATION THEORY

It will be recalled that Darwin, although depending upon the ever-present fluctuating variations as the material for natural selection to work upon, recognized the occasional occurrence of ' sports" or "saltatory variations " These, however, seemed to him to be so rare in nature as to offer no adequate basis for selection During the latter part of the nineteenth century several investigators, feeling the inadequacy of fluctuating variations to produce qualitatively new characters, decided to make a more careful examination of animals and plants in nature in order to discover whether saltatory variations might not be of more frequent occurrence than Darwin had supposed

In England William Bateson collected a large number of instances of a type of variation which he called *discontinuous* in contradistinction to the *continuous* type which we have been calling fluctuations Such variations, instead of being in a closely graded series with the typical variations of a species, were frequently quite sharply different from the majority Although no experiments were conducted in order to test the heritability of these "discontinuous variations, ' it is probable that some of them were "mutations ' in the sense of De Vries

At about the same time Hugo De Vries in Holland, partially as the result of his rediscovery of Mendel's work and his confirmation of the latter's laws of heredity, became convinced that new species arise not by the accumulation, through natural selection, of minute fluctuating variations, but by the sudden appearance in one generation of fully formed new elementary species He began a systematic research for species of plants in nature that were giving rise to new species Many species were examined in their natural surroundings and were then brought into the experimental garden for more careful observation but for a long time the search for a species throwing off new elementary species was unsuccessful Finally, however, in a field near Hilversum, in the vicinity of Amsterdam, he found what seemed to him to be just the kind of plant he had been looking for in the evening primrose (*Oenothera lamarckiana*)

"Lamarck's evening primrose" (Fig 75), says De Vries, "is a stately plant with a stout stem attaining often a height of 1 6 meters and more When not crowded the main stem is surrounded by a large

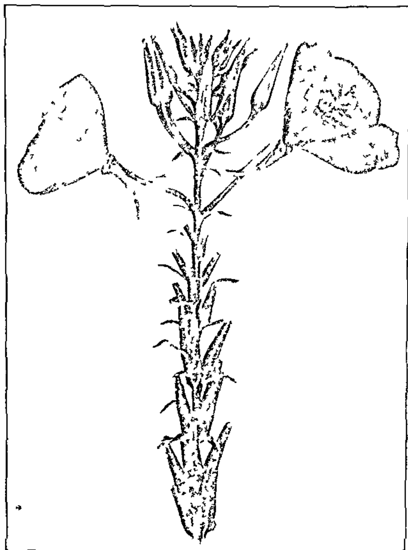


FIG 75 —*Oenothera lamarckiana* the original type used by De Vries in his experiments This is the stock from Hilversum, from which arose in successive generations a series of mutants (*From De Vries*)

circle of smaller branches, growing upwards from its base so as to form a dense brush The flowers are large and bright yellow attracting immediate attention even from a distance They open toward evening, as the name indicates, and are pollinated by bumble-bees and moths"

On account of the classic character of De Vries's mutants of *Oenothera lamarckiana* we shall follow his own detailed description of the more significant of these

NEW SPECIES (MUTANTS) OF *OENOTHERA*[1]

HUGO DE VRIES

This striking species (*Oenothera lamarckiana*) was found in a locality near Hilversum, in the vicinity of Amsterdam, where it grew in some thousands of individuals Ordinarily biennial, it produces rosettes in the first, and stems in the second year Both the stems and the rosettes were at once seen to be highly variable, and soon distinct varieties could be distinguished among them

The first discovery of this locality was made in 1886 Afterwards I visited it many times often weekly or even daily during the first few years, and always at least once a year up to the present time This stately plant showed the long sought peculiarity of producing a number of new species every year Some of them were observed directly on the field, either as stems or as rosettes The latter could be transplanted into my garden for further observation and the stems yielded seeds to be sown under like control Others were too weak to live a sufficiently long time in the field They were discovered by sowing seed from indifferent plants of the wild locality in the garden A third and last method of getting still more new species from the original strain was the repetition of the sowing process by saving and sowing the seed which ripened on the introduced plants These various methods have led to the discovery of over a dozen new types never previously observed or described

Leaving the physiological side of the relations of these new forms for the next lecture it would be profitable to give a short description of the several novelties To this end they may be combined under five different heads, according to their systematic value The first head includes those which are evidently to be considered as varieties

[1] From H De Vries *Species and Varieties* (copyright 1904) Used by special permission of the publishers The Open Court Publishing Company

in the narrower sense of the word, as previously given The second and third heads indicate the real progressive elementary species, first those which are as strong as the parent species, and secondly a group of weaker types, apparently not destined to be successful Under the fourth head I shall include some inconstant forms, and under the last head those that are organically incomplete

Of varieties with a negative attribute, or real retrograde varieties I have found three, all of them in a flowering condition in the field I have given them the names of *laevifolia*, *brevistylis* and *nannella*

The *laevifolia*, or smooth leaved variety, was one of the very first deviating types found in the original field This was in the summer of 1887, seventeen years ago It formed a little group of plants growing at some distance from the main body, in the same field I found some rosettes and some flowering stems and sowed some seed in the fall The variety has been quite constant in the field neither increasing in number of individual plants nor changing its place, though now closely surrounded by other *lamarckianas* In my garden it has proved to be constant from seed never reverting to the original *lamarckiana*, provided intercrossing was excluded

It is chiefly distinguished from Lamarck s evening primrose by its smooth leaves, as the name indicates The leaves of the original form show numerous sinuosities in their blades, not at the edge, but anywhere between the veins The blade shows numbers of convexities on either surface, the whole surface being undulated in this manner, it lacks also the brightness of the ordinary evening primrose or *Oenothera biennis*

These undulations are lacking or at least very rare on the leaves of the new *laevifolia* Ordinarily they are wholly wanting, but at times single leaves with slight manifestations of this character may make their appearance They warn us that the capacity for such sinuosities is not wholly lost, but only lies dormant in the new variety It is reduced to a latent state, exactly as are the apparently lost characters of so many ordinary horticultural varieties

Lacking the undulations, the *laevifolia*-leaves are smooth and bright They are a little narrower and more slender than those of the *lamarckiana* The convexities and concavities of leaves are a useful character in dry seasons, but during wet summers, such as those of the last few years, they must be considered as very harmful, as they retain some of the water which falls on the plants, prolonging the action of the water on the leaves This is considered by some writers

to be of some utility after slight showers, but was observed to be a source of weakness during wet weather in my garden, preventing the leaves from drying Whether the *laevifolia* would do better under such circumstances, I have, however, omitted to test

The flowers of the *laevifolia* are also in a slight degree different from those of *lamarckiana* The yellow color is paler and the petals are smoother Later, in the fall, on the weaker side branches these differences increase The *laevifolia* petals become smaller and are devoid of the emargination at the apex, becoming ovate instead of obcordate This shape is often the most easily recognized and most striking mark of the variety In respect to the reproductive organs the fertility and abundance of good seed, the *laevifolia* is by no means inferior or superior to the original species

O brevistylis, or the short styled evening primrose, is the most curious of all my new forms It has very short styles, which bring the stigmas only up to the throat of the calyx tube, instead of upwards of the anthers The stigmas themselves are of another shape, more flattened and not cylindrical The pollen falls from the anthers abundantly on them, and germinates in the ordinary manner

The ovary which in *lamarckiana* and in all other new forms is wholly underneath the calyx tube, is here only partially so This tube is inserted at some distances under its summit The insertion divides the ovary into two parts an upper and a lower one The upper part is much reduced in breadth and somewhat attenuated, simulating a prolongation of the base of the style The lower part is also reduced, but in another manner At the time of flowering it is like the ovary of *lamarckiana*, neither smaller nor larger *But it is only reached by* very few pollen-tubes, and is therefore always very incompletely fertilized It does not fall off after the fading away of the flower, as unfertilized ovaries usually do, neither does it grow out, nor assume the upright position of normal capsules It is checked in its development, and at the time of ripening it is nearly of the same length as in the beginning Many of them contain no good seeds at all, from others I have succeeded in saving only a hundred seeds from thousands of capsules

These seeds, if purely pollinated, and with the exclusion of the visits of insects, reproduce the variety entirely and without any reversion to the *lamarckiana* type

Correlated with the detailed structures is the form of the flower-buds They lack the high stigma placed above the anthers, which in

the *lamarckiana*, by the vigorous growth of the style, extends the calyx and renders the flower bud thinner and more slender Those of the *brevistylis* are therefore broader and more swollen It is quite easy to distinguish the individuals by this striking character alone, although it differs from the parent in other particulars

The leaves of the *O brevistylis* are more rounded at the tip, but the difference is only pronounced at times, slightly in the adult rosettes, but more clearly on the growing summits of the stems and branches By this character the plants may be discerned among the others some weeks before the flowers begin to show themselves

But the character by which the plants may be most easily recog nized from a distance in the field is the failure of the fruits They were found nearly every year in varying, but always small numbers

Leaving the short styled primrose, we come now to the last of our group of retrograde varieties This is the *O nannella*, or the dwarf and is a most attractive little plant It is very short of stature, reaching often a height of only 20–30 cm , or less than one fourth of that of the parent. It commences flowering at a height of 10–15 cm , while the parent form often measures nearly a meter at this stage of its development Being so very dwarfed the large flowers are all the more striking They are hardly inferior to those of the *lamarckiana* and agree with them in structure When they fade away the spike is rapidly lengthened and often becomes much longer than the lower or vegetative part of the stem

The dwarfs are one of the most common mutations in my garden and were observed in the native locality and also grown from seeds saved there Once produced they are absolutely constant. I have tried many thousands of seeds from various dwarf mutants, and never observed any trace of reversion to the *lamarckiana* type I have also cultivated them in successive generations with the same result. In a former lecture we have seen that contrary to the general run of horticultural belief, varieties are as constant as the best species, if kept free from hybrid admixtures This is a general rule, and the ex ceptions or cases of atavism, are extremely rare In this respect it is of great interest to observe that this constancy is not an acquired quality, but is to be considered as innate, because it is already fully developed at the very moment when the original mutation takes place

From its first leaves to the rosette period, and through this to the lengthening of the stem, the dwarfs are easily distinguished from any other of their congeners. The most remarkable feature is the shape

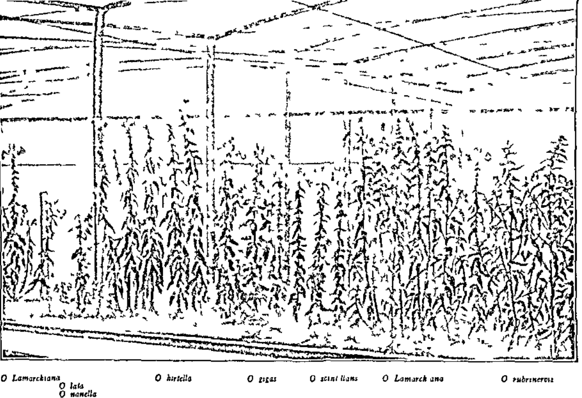


Fig. 76.—A series showing *Oenothera lamarckiana* and several of its mutants growing side by side, illustrating differ-

of the leaves They are broader and shorter, and especially at the base they are broadened in such a way as to become apparently sessile The stalk is very brittle, and any rough treatment may cause the leaves to break off The young seedlings are recognizable by the shape of the first two or three leaves, and when more of them are produced, the rosettes become dense and strikingly different from others Later leaves are more nearly like the parent type, but the petioles remain short The bases of the blades are frequently almost cordate, the laminae themselves varying from oblong ovate to ovate in outline

The stems are often quite unbranched, or branched only at the base of the spike Strong secondary stems are a striking attribute of the *lamarckiana* parent, but they are lacking, or almost so in the dwarfs The stem is straight and short, and this, combined with the large crown of bright flowers, makes the dwarfs eminently suitable for bed or border plants Unfortunately they are very sensitive, especially to wet weather

Oenothera gigas and *O rubrinervis*, or the giant, and the red veined evening primroses, are the names given to two robust and stout species, which seem to be equal in vigor to the parent plant, while diverging from it in striking characters Both are true elementary species, differentiated from *lamarckiana* in nearly all their organs and qualities, but not showing any preponderating character of a retrograde nature Their differences may be compared with those of the elementary species of other genera, as for instance, of *Draba*, or of violets as will be seen by their description

The giant evening primrose, though not taller in stature than *O lamarckiana*, deserves its name because it is so much stouter in all respects The stems are robust, often with twice the diameter of *lamarckiana* throughout The internodes are shorter, and the leaves more numerous, covering the stems with a denser foliage This shortness of internodes extends itself to the spike, and for this reason the flowers and fruits grow closer together than on the parent plant. Hence the crown of bright flowers, opening each evening, is more dense and more strikingly brilliant, so much the more so as the individual flowers are markedly larger than those of the parents In connection with these characters, the flower-buds are seen to be much stouter than those of *lamarckiana* The fruits attain only half the normal size, but are broader and contain fewer, but larger seeds

The *rubrinervis* is in many respects a counterpart to the *gigas*, but its stature is more slender The spikes and flowers are those of the *lamarckiana*, but the bracts are narrower Red veins and red streaks on the fruits afford a striking differentiating mark, though they are not absolutely lacking in the parent-species A red hue may be seen on the calyx, and even the yellow color of the petals is somewhat deepened in the same way Young plants are often marked by the pale red tinge of the mid veins, but in adult rosettes, or from lack of sunshine, this hue is often very faint

The leaves are narrow, and a curious feature of this species is the great brittleness of the leaves and stems, especially on annual individuals, for example, on those that make their stem and flowers in the first year High turgidity and weak development of the mechanical and supporting tissues are the anatomical cause of this deficiency the bast fibres showing thinner walls than those of the parent type under the microscope Young stems of *rubrinervis* may be broken off by a sharp stroke, and show a smooth rupture across all the tissues while those of *lamarckiana* are very tough and strong

Both the giant and the red veined species are easily recognized in the rosette-stage The very young seedlings of the latter are not clearly differentiated from the *lamarckiana* and often a dozen leaves are required before the difference may be seen Under ordinary circumstances the young plants must reach an age of about two months before it is possible to discern their characters, or at least before these characters have become reliable enough to enable us to judge of each individual without doubt But the divergencies rapidly become greater The leaves of *O gigas* are broader of a deeper green the blade more sharply set off against the stalk, the whole rosettes becoming stout and crowded with leaves Those of *O rubrinervis* on the contrary are thin, of a paler green and with a silvery white surface, the blades are elliptic, often being only 2 cm or less in width They are acute at the apex and gradually narrowed into the petiole

It is quite evident that such pale narrow leaves must produce smaller quantities of organic food than the darker green and broad organs of the *gigas* Perhaps this fact is accountable partly, at least, for the more robust growth of the giant in the second year Perhaps also some relation exists between this difference in chemical activity and the tendency to become annual or biennial The *gigas*, as a rule, produces far more and the *rubrinervis* far less biennial plants than the *lamarckiana* Annual culture for the one is as unreliable as

biennial culture for the other *Rubrinervis* may be annual in apparently all specimens, in sunny seasons which would allow a large part of the *gigas* to remain in the state of rosettes during the entire first summer It would be very interesting to obtain a fuller insight into the relation of the length of life to other qualities, but as yet the facts can only be detailed as they stand

Both of these stout species have been found quite constant from the very first moment of their appearance I have cultivated them from seed in large numbers, and they have never reverted to the *lamarckiana* From this they have inherited the mutability or the capacity of producing in their turn new mutants But they seem to have done so incompletely changing in the direction of more absolute constancy This was especially observed in the case of *rubrinervis*, which is not of such rare occurrence as *O gigas*, and which it has been possible to study in large numbers of individuals So for instance 'the red veins' have never produced any dwarfs, notwithstanding they are produced very often by the parent type And in crossing experiments the red veins gave proof of the absence of a mutative capacity for their production

[Besides the mutants just described there occurred two weak forms that could survive only if reared under protection and would have failed to survive in nature Here we have a place for the action of natural selection but operating with mutations instead of with fluctuating variations These two mutants are "the whitish and the oblong leaved evening primroses or the *Oenothera albida* and *oblonga* '

All of the mutants so far mentioned are constant forms that breed true to type Certain other types were either incapable of being bred or else were decidedly inconstant *Oenothera lata* had only pistillate flowers and therefore could not be fertilized by pollen of the same mutant *Oenothera scintillans* and *O elliptica* are fertile to their own pollen, but produce progeny only partly like the parent, the rest reverting to the original type, *Oenothera lamarckiana*]

SUMMARY OF DE VRIES'S MUTATION THEORY[1]

THOMAS HUNT MORGAN

We may now proceed to examine the evidence from which De Vries has been led to the general conclusions given in the preceding pages De Vries found at Hilversum, near Amsterdam, a locality

[1] T H Morgan *Evolution and Adaptation* (1903) Used by special permission of the publishers, The Macmillan Company

where a number of plants of the evening primrose, *Oenothera lamarckiana*, grow in large numbers This plant is an American form that has been imported into Europe It often escapes from cultivation, as is the case at Hilversum, where for ten years it had been growing wild. Its rapid increase in numbers in the course of a few years may be one of the causes that has led to the appearance of a mutation period. The escaped plants showed fluctuating variations in nearly all of their organs They also had produced a number of abnormal forms Some of the plants came to maturity in one year, others in two, or in rare cases, in three, years

A year after the first finding of these plants De Vries observed two well-characterized forms, which he at once recognized as new elementary species One of these was *O brevistylis*, which occurred only as female plants The other new species was a smooth leafed form with a more beautiful foliage than *O lamarckiana* This is *O laevifolia* It was found that both of these new forms bred true from self fertilized seeds At first only a few specimens were found, each form in a particular part of the field, which looks as though each might have come from the seeds of a single plant

These two new forms as well as the common *O lamarckiana*, were collected, and from these plants there have arisen the three groups of families of elementary species that De Vries has studied In his garden other new forms also arose from those that had been brought under cultivation The largest group and the most important one is that from the original *O lamarckiana* form The accompanying table shows the mutations that arose between 1887 and 1899 from these plants The seeds were selected in each case from self fertilized plants of the *lamarckiana* form, so that the new plants appearing in each horizontal line are the descendants in each generation of *lamarckiana* parents It will be observed that the species *O oblonga*, appeared again and again in considerable numbers and the same is true for several of the other forms also Only the two species, *O gigas* and *O scintillans*, appeared very rarely (Fig 77)

Thus De Vries had in his seven generations about fifty thousand plants, and about eight hundred of these were mutations When the flowers of the new forms were artificially fertilized with pollen from the flowers of the same plant, or of the same kind of plant, they gave rise to forms like themselves, thus showing that they are true elementary species It is also a point of some interest to observe that all these forms differed from each other in a large number of particulars.

Only one form, *O scintillans*, that appeared eight times, is not constant as are the other species When self fertilized its seeds produce always three other forms, *O scintillans*, *O oblonga*, and *O lamarckiana* It differs in this respect from all the other elementary species, which mutate not more than once in ten thousand individuals

Generations	O gigas	O albida	O oblonga	O rubrinervis	O Lamarckiana	O nanella	O lata	O scintillans
Gen 8 1899		5	1	0	1700	21	1	
Gen 7 1898			9	0	3700	11		
Gen 6 1897		11	29	3	1800	9	5	1
Gen 5 1896		25	135	20	8000	49	142	6
Gen 4 1895	1	15	176	8	14000	60	73	1
Gen. 3 1890–91				1	10000	3	3	
Gen 2 1888–89					15000	5	5	
Gen. 1 1886–87					9			
	Mutants and Number observed in different years				O Lamarckiana The mutating stem form	Mutants and Number observed in different years		

FIG 77 —Diagram showing in condensed form the genealogy of the *Oenothera Lamarckiana* family and its various mutants during successive years The numbers under each type represent the number of new types observed each year (*From Tower*)

From the seeds of one of the new forms, *O laevifolia*, collected in the field, plants were reared, some of which were *O lamarckiana* and others *O laevifolia* They were allowed to grow together, and their descendants gave rise to the same forms found in the *lamarckiana*

family, described above, namely, *O lata, elliptica, nannella, rubrinervis*, and also two new species, *O spatulata* and *leptocarpa*

In the *lata* family, only female flowers are produced, and, therefore, in order to obtain seeds they were fertilized with pollen from other species Here also appeared some of the new species already mentioned, namely, *albida, nannella, lata, oblonga rubrinervis*, and also two new species, *elliptica* and *subovata*

De Vries also watched the field from which the original forms were obtained, and found there many of the new species that appeared under cultivation These were found, however, only as weak young plants that rarely flowered Five of the new forms were seen either in the Hilversum field, or else raised from seeds that had been collected there These facts show that the new species are not due to cultivation, and that they arise year after year from the seeds of the parent form, *O lamarckiana*

Conclusions —From the evidence given in the preceding pages it appears that the line between fluctuating variations and mutations may be sharply drawn If we assume that mutations have furnished the material for the process of evolution, the whole problem appears in a different light from that in which it was placed by Darwin when he assumed that the fluctuating variations are the kind which give the material for evolution

From the point of view of the mutation theory, species are no longer looked upon as having been slowly built up through the selection of individual variations, but the elementary species at least, appear at a single advance, and fully formed This need not necessarily mean that great changes have suddenly taken place, and in this respect the mutation theory is in accord with Darwin's view that extreme forms that rarely appear, "sports," have not furnished the material for the process of evolution

As De Vries has pointed out, each mutation may be different from the parent form in only a slight degree for each point, although all the points may be different The most unique feature of these mutations is the constancy with which the new form is inherited It is this fact, not previously fully appreciated, that De Vries's work has brought prominently into the foreground There is another point of great interest in this connection Many of the groups that Darwin recognized as varieties correspond to the elementary species of De Vries These varieties, Darwin thought, are the first stages in the formations of species, and, in fact, cannot be separated from species in most cases The main difference between the selection theory and

the mutation theory is that the one supposes these varieties to arise through selection of individual variations, the other supposes that they have arisen spontaneously and at once from the original form The development of these varieties into new species is again supposed, on the Darwinian theory, to be the result of further selection, on the mutation theory, the result of the appearance of new mutations

In consequence of this difference in the two theories, it will not be difficult to show that the mutation theory escapes some of the gravest difficulties that the Darwinian theory has encountered Some of the advantages of the mutation theory may be briefly mentioned here

1 Since the mutations appear fully formed from the beginning there is no difficulty in accounting for the incipient stages in the development of an organ, and since the organ may persist, even when it has no value to the race, it may become further developed by later mutations and may come to have finally an important relation to the life of the individual

2 The new mutations may appear in large numbers, and of the different kinds those will persist that can get a foothold On account of the large number of times that the same mutations appear, the danger of becoming swamped through crossing with the original form will be lessened in proportion to the number of new individuals that arise

3 If the time of reaching maturity in the new form is different from that in the parent forms, then the new species will be kept from crossing with the parent form, and since this new character will be present from the beginning, the new form will have much better chances of surviving than if a difference in time of reaching maturity had to be gradually acquired

4 The new species that appear may be in some cases already adapted to live in a different environment from that occupied by the parent form, and if so, it will be isolated from the beginning, which will be an advantage in avoiding the bad effects of intercrossing

5 It is well known that the differences between related species consist largely in differences of unimportant organs, and this is in harmony with the mutation theory, but one of the real difficulties of the selection theory

6 Useless or even slightly injurious characters may appear as mutations, and if they do not seriously affect the perpetuation of the race, they may persist

LATER INVESTIGATIONS OF MUTATIONS

Since the publication of De Vries's classic investigations a large amount of attention has been paid both by botanists and by zoologists to the subject of mutations Some of the investigators notably B M Davis, went far toward discrediting the whole of the exceptionally careful work of De Vries by claiming that *Oenothera lamarckiana* is of hybrid origin It was pointed out that the form worked with is a domestic type escaped from cultivation and that there is nowhere in the known world any wild species comparable with it It is supposed to have been brought to Europe from America many years ago but there is no such species in America today Davis claims that he has succeeded in producing, by crossing two American wild species a hybrid form distinctly resembling *Oenothera lamarckiana* and that when inbred this hybrid produces offspring showing various combinations of the two parent species that are not unlike some of the mutants observed by De Vries Jeffreys has also pointed out that the pollen grains of *Oenothera lamarckiana* exhibit a high percentage of sterility which he believes to be a stigma of hybridity The general tenor of this type of destructive criticism is to invalidate the whole mutation theory as developed by De Vries and to reduce his mutants to the level of mere Mendelian recombinations of characters once introduced from two or more parental species

The large amount of work on the cytology of *Oenothera* by Gates and others has, however, served to show that the mutants of De Vries are more than hybrid segregates Moreover, the beautiful work of Blakeslee on the Jimson weed (*Datura*) and the work of many other botanists whose findings are reported by Gates in a contribution quoted below, serve to indicate that the type of evolutionary behavior first observed in *Oenothera* is by no means exceptional but is probably a common thing at least among plants and may be commoner than we at present know in animals It may be said by way of anticipation of Gates' detailed account that nearly all of the mutations observed in various species of plants may be definitely correlated with observable changes in the chromosomes of the germ cells, involving changes in number or changes in arrangement of these nuclear elements

While the botanists busied themselves with their type of mutations the zoologists, especially T H Morgan and his able collaborators, were making discoveries of equal moment in connection with their studies of the mechanism of Mendelian heredity in *Drosophila* As has al

ready been shown in previous chapters, hundreds of new hereditary types arose, apparently spontaneously, in pure-pedigreed stock Each new type is designated a mutant, and the cause of the changed hereditary condition is not a gross chromosomal change, but an invisible change at a definite point in a definite chromosome, whose cause is unknown but whose location can be exactly determined Such mutations are known as gene mutations Like the mutants of *Oenothera* these *Drosophila* mutants do not differ from the parent species in just one or two characters but in several or many characters Usually some one or two characters in any given mutant are especially characteristic, and these serve to give a name to each mutant and make it easier to identify them Both morphological and physiological characters are involved in these mutants, and every part of the body may be involved Sometimes the change is so slight as to require an eye sensitized by much training to detect them It may happen for example that two mutants of the eye are so much alike that the human eye is not sufficiently keen to tell them apart, but they may be distinguished by differences in their hereditary behavior A large percentage of the mutants discovered in *Drosophila* are "lethals," which means that the change is decidedly for the worse under the prevailing conditions of life, and that they render the individual unfit to live Possibly under decidedly different conditions some of these lethal mutants might be better adapted than the normal individuals A further discussion of the rôle of mutants in evolution will be given in a later connection

The following two rather technical, but very interesting, discussions as to the nature, causes, and significance of mutations are from two men who are recognized as perhaps the leaders in the two branches of mutation study R R Gates has done a large amount of important work especially upon the cytology of *Oenothera*, and H J Muller has done and is still doing much to enrich our understanding of the mutational phenomena exhibited by *Drosophila* While these two workers do not agree as to the relative emphasis that should be placed upon the two types of mutation, it is obvious that both types are of very great importance in evolution

THE NEO-MUTATIONIST POSITION

R RUGGLES GATES

Since the original work of De Vries the subject of mutation in Oenothera has advanced in many directions and the explanation of the phenomena has taken on various aspects Mutation has become

essentially a cell problem. Cytological investigations have shown that many of the mutations are concerned with new chromosome numbers, and the precise nature of the change which has led to the appearance of forms with a new number is known with more or less certainty in the various cases. The new number is in each case present throughout the plant and will be found whether the chromosomes be counted in growing petals, root tips or anthers. These discoveries led in 1915 to the conception that each mutation with its new external characters is the result of nuclear changes transmitted by mitosis to every cell of the plant during development. A fundamental advance in the analysis of mutations has thus been made.

Mutations can now be classified into two types. (1) Mutations which are inherited as Mendelian differences, and which may be looked upon provisionally as the result of a chemical change in one gene or locus of a chromosome. The great majority of the mutations in Drosophila are of this type. On the other hand very few Mendelian mutations are known in Oenothera. The two best known are *rubricalyx*, which is a dominant in crosses and *brevistylis* which is inherited as a recessive. (2) Mutations resulting from a visible nuclear change involving a new number of chromosomes. Probably the majority of Oenothera mutations belong here. Similar mutations have been discovered in Drosophila and also in Datura. Examination of the chromosome numbers in related species of wild and cultivated plants shows that such changes have been of relatively frequent occurrence in the evolution of many plant genera but they appear to be less common in animals.

CHROMOSOME MUTATIONS

The mutations with new chromosome numbers which are particularly characteristic of Oenothera may be classified into three types —(1) *trisomic forms* i e mutations with one or sometimes two extra chromosomes ($2n+1$) (2) *triploid* forms ($3n$) and (3) *tetraploid* ($4n$) forms. Other forms with different numbers as 20 or 30 may be regarded as derivatives from these types.

Trisomic forms are known to arise through non disjunction or a reduction division in which both members of one pair of chromosomes

from *O lamarckiana* they give the two parental types of offspring having presumably 14 and 15 chromosomes Since there are only seven pairs of chromosomes these trisomic types can not all be accounted for by duplication of a different chromosome in each case

The genetic relationships between these trisomic mutants are also interesting and peculiar Thus *lata* can give rise to *scintillans* in its offspring, and *scintillans* can similarly produce *lata* Also *lata* (pollinated from *lamarckiana*) can give rise to several other trisomic mutations Many of these relationships can be explained by the assumption of double non disjunction, i e, both members of one chromosome pair entering one germ cell while both members of another pair enter the opposite cell It is highly probable that such cases occur Thus germ cells would be produced with the chromosome content AACDEFG and BBCDEFG It can be shown that by such a process one trisomic mutation could give rise to another in its offspring It is very probable that *lata* is a primary trisomic mutation, e g, $\frac{AABCDEFG}{ABCDEFG}$, i e, with three A chromosomes, while some other trisomic $(2n+1)$ mutations are probably secondary, e g, $\frac{AABCDEFG}{ACCDEFG}$, i e, with for example three A and three C chromosomes but only one B chromosome All such irregular chromosome distributions are probably enabled to occur through a weakness in the attraction which normally leads to close pairing of homologous chromosomes during synapsis or on the heterotypic spindle There is much evidence of variation in the strength of this attraction in Oenothera

Cleland has recently found that the chromosomes in various Oenothera species retain their end to-end connections even on the heterotypic spindle He has also shown that in several species the arrangement of the chromosomes is more or less constant and characteristic during the stages immediately preceding the reduction division Thus in *O franciscana* four of the chromosomes form a ring while the other ten are arranged in five ring pairs which are at first linked to the circle of four in a definite way In a form called *O franciscana sulphurea*, which is derived from *O biennis*×*franciscana* 12 chromosomes end to-end form a circle and the other two form a pair which is at first linked round the larger chain of 12, and this arrangement is said to be constant Thus in the derived form a rearrangement of the chromosomes with relation to each other has taken place Cleland finds similar fixed arrangements in other species.

Thus in a race identified with *O muricata* the 14 chromosomes all form a single circle, in *O biennis* they are usually in two interlooking circles one with 6 and the other with 8 chromosomes while in the mutant *oblonga* with 15 chromosomes the arrangement is more variable but frequently shows a ring of 5 single chromosomes with 5 pairs attached to it In a trisomic mutant from *O rubricalys*×*hewettii* a varying number of ring pairs was found by the writer If the relative constancy of these arrangements is confirmed, it will show an essentially new type of integration in nuclear structure, that is a fixed positional arrangement of the chromosomes in the nucleus with relation to one another This will also confirm the hypothesis of the writer years ago that the homologous maternal and paternal chromosomes in Oenothera are usually arranged alternately on the spireme thread before the reduction division The fact that also, as observed by the writer in 1908, pairs of chromosomes are frequently detached from the rest of the spireme in certain forms at an early stage of diakinesis would make it easier for double non-disjunction to occur on the heterotypic spindle in these forms The further study of the chromosome arrangements in hybrids and mutants will throw more light on these rearrangements and perhaps also on the nature of the forces which bring them about Such rearrangements without change of number, if they prove to be constant, are to be considered as mutations of another kind

Whether non disjunction has played a part in the appearance of species in nature with a different chromosome number is as yet uncertain But there are certain genera, such as Carex, in which the haploid numbers usually increase by one from species to species Heilborn suggests that this may have happened by non-disjunction as in *Oenothera lata*, followed by the division of the extra chromosome to form a pair

Polyploidy —An increase in the chromosome number by multiples of the haploid number (polyploidy) is a phenomenon of considerable phylogenetic significance in plants, although it appears to be relatively uncommon in animals There has been a burst of new knowledge on this subject in the last few years Since the original mutant *Oenothera gigas* has been shown to be tetraploid and *semigigas* mutations triploid we have an experimental basis for the interpretation of all such cases It appears probable that the triploid condition in Oenothera arises through the union of two male nuclei with the egg, as this condition has been actually observed in *O lamarckiana* by Ishikawa and in other plants as well

A difference of opinion has long existed as to whether *O gigas* arose from the fusion of two diploid cells or from a suspended mitosis with division of the chromosomes in the fertilized egg I am still inclined to adhere to the latter view as more probable, with perhaps a sudden lowering of temperature just after fertilization as the cause Although it is a fact that diploid germ cells do sometimes occur diploid pollen grains are not known to be viable in plants

The frequency of polyploidy in flowering plants, and also in other groups of plants, is one of the surprises of recent years Not only does the condition occur in such cultivated plants as pineapples, bananas mulberries, wheat oats, sugar cane, dahlias, and tobacco, but also in such genera of wild plants as the roses, maples, chrysanthemums, Erigeron, Hieracium, Rumex, Rubus, Crataegus, Spiranthus, and a number of others The multiplication of chromosome sets runs as high as $8n$ in Rosa and in Acer, and even as high as $10n$ in certain species of Rumex (80 chromosomes) and chrysanthemums (90 chromosomes) Such a widespread phenomenon must be of fundamental significance in the evolution of the genera in which it occurs The higher degrees of polyploidy are probably often connected with hybridization, but there the higher chromosome numbers are usually accompanied by apogamous (asexual) reproduction, which renders constant even forms with an unbalanced chromosome number This is true even of the triploid mulberries and Erigerons, etc In every case of polyploidy the higher numbers have not arisen gradually by the addition of single chromosomes, but one or more complete sets have been added each time and the process is a mutation involving considerable discontinuity

That still other kinds of chromosome change occur, is shown both from experimental work and by comparison of the chromosomes of related species Thus transverse segmentation of all chromosomes has taken place in *Primula kewensis*, and end to-end fusion of certain pairs has evidently occurred in some species of Drosophila In the Japanese violets there is some indication that the small number of large chromosomes in certain species may have been derived by the fusion of smaller chromosomes found in other species A process suggesting transverse fragmentation of certain pairs of long chromosomes appears to have occurred in various genera of Liliaceae Further study will no doubt throw light on the nature of these processes It appears already that the passage from one genus to another has not infrequently been marked by a visible change in the chromatin mor

phology of the nucleus Such alterations in the conformation of the nuclear material are to be regarded as germinal changes, even though they are not accompanied by external changes in the organism

MUTATION[1]

H J MULLER

Beneath the imposing building called ' Heredity" there has been a dingy basement called "Mutation ' Lately the searchlight of genetic analysis has thrown a flood of illumination into many of the dark recesses there, revealing some of them as ordinary rooms in no wise different from those upstairs, that merely need to have their blinds flung back, while others are seen to be subterranean passageways of quite a different type In other words, the term mutation originally included a number of distinct phenomena, which, from a genetic point of view, have nothing in common with one another They were classed together merely because they all involved the sudden appearance of a new genetic type Some have been found to be special cases of Mendelian recombination, some to be due to abnormalities in the distribution of entire chromosomes, and others to consist in changes in the individual genes or hereditary units It seems incumbent upon us however, in the interests of scientific clarity, to agree to confine our use of the term mutation to one coherent class of events The usage most serviceable for our modern purpose would be to limit the meaning of the term to the cases of the third type—that is, to real changes in the gene This would also be most in conformity with the spirit of the original usage, for even in the earlier days, mutations were conceived of as fundamental changes in the hereditary constitution and there were never intentionally included among them cases merely involving redistribution of hereditary units—when these cases were recogniz able as such In accordance with these considerations, our new defini tion would be "mutation is alteration of the gene And alteration as here used, is of course understood to mean a change of a transmissible or at least of a propagable, sort

In thus trimming down the scope of our category of mutation we do not deprive it of the material of most fundamental evolutionary significance For all changes due to the redistribution of individual genes or of groups of genes, into new combinations, proportions or quantities, are obviously made possible only by the prior changes tha

[1] Reprinted from *Eugenics Genetics and the Family* Vol I (1923) Courtesy of the Williams and Wilkins Company

make these genes differ from each other in the first place It should in addition be noted that changes due merely to differences in the gross proportions of entire groups of genes must be relatively incapable of that delicate adjustment which is required for evolutionary adaptation And as to the question, frequently raised, whether all evolution is ultimately due to mutation, this is necessarily answered in the affirmative by our definitions of the gene and of mutation, which designate the gene as any unit of heredity, and mutation as any transmissible change occurring in the gene The question of the basic mechanism of evolution thus becomes transferred to the problem of the character, frequency, and mode of occurrence of mutation, taken in this precise, yet comprehensive sense And since eugenics is a special branch of evolutionary science it must be equally concerned with this problem

In choosing the body of data wherewith to attack these questions of mutation, in their new form, it must unfortunately be recognized that the results with the evening primrose, Oenothera, although they formed the backbone of the earlier mutation theory, can no longer be regarded as having a direct bearing on the modern problem, since they cannot be shown to be due directly to changes in the genes Certain of them such as gigas, lata, scintillans, etc , have been proved by Geerts, Lutz, Gates, and others, to be due to abnormalities in the apportionment of the chromosomes Very valuable information on the genetics of cases of this sort is now being obtained, especially in the work of Blakeslee Belling, and Farnham on much clearer cases of similar character in the Jimson weed, and, finally, in the work of Bridges on the fruit fly Drosophila Most of the other so-called mutations in the evening primrose appear to be due to the normal hereditary processes of segregation and crossing over, working on a genetic constitution of a special type Evidence for this was obtained in my analysis of the analogous case existing in the fly Drosophila, as follows It had previously been shown by de Vries, and further elaborated by Renner, that germ cells or individuals of Oenothera bearing certain genes always died, in such a way that all the surviving individuals were heterozygous (hybrid) in regard to these genes I later showed, through work on Drosophila, that when such a condition (there called "balanced lethal factors ') exists, the situation tends to become still further complicated through the presence of other heterozygous genes, which are linked to those which cause death When one or a group of these non lethal genes crosses over (separates) from the lethals, as they occasionally do, they may become homozygous producing a visible effect Thus new types of individuals appear which may be ascribed to "mutation," whereas they

are really due to crossing over The work of Frost on stocks has shown that a precisely analogous situation exists in that form also, and G H Shull is obtaining direct evidence for the same conclusion in the evening primrose itself In any event, it must be granted that so long as this interpretation cannot be definitely refuted, these variations can not be used as examples on which to base our theory of gene change In place, then, of the elaborate system of conclusions which has derived its support chiefly from the results in the evening primrose, it will be necessary for our present theory of gene change to erect an independent structure, built upon an entirely new basis

The data upon which the new theory must be built consist of two main sorts, which may be called direct and indirect. (1) In the cases giving the direct evidence, the occurrence of the gene change can be proved, and it is possible to exclude definitely all alternative explanations, such as contamination of the material, emergence of previously "latent" factors, non-disjunction, etc. So far, the only considerable body of such evidence is that gotten in the Drosophila work, where mutations have (in this sense) been actually observed in at least 100 loci. Considered collectively, however, there exist in other organisms enough scattered data to afford ample corroborative evidence for the generality of occurrence of mutations like those observed in the Drosophila work. In addition several specially mutable genes have been found in a number of plants (as well as in Drosophila) that are giving highly valuable information along their particular lines And a number of selection experiments that have been performed on non segregating lines of various organisms have also given us direct evidence, if not of the frequency, then at least of the infrequency, of mutations (2) As for the indirect data, these may be gotten by examination of Mendelian factor-differences of all kinds, on the assumption that they *must have* arisen through mutation *Although this assumption can be* shown to be fully justified, these cases cannot provide information concerning the manner of origin of the mutants, nor can they furnish a reliable index of the frequency of mutations, since the mutant genes may have been subjected to an unknown amount of selective elimination or selective propagation before the observations were taken As for the still more indirect data, derived from studies of phylogenetic series and comparisons between different species genera, etc., these occasionally give suggestive results, but where crosses cannot be made or where the differences cannot be traced down to the individual genes, such facts can seldom lead to trustworthy genetic conclusions.

On these various data, duly weighted, we may found our new muta

tion theory We know nothing, as yet, about the mechanism of mutation, or about the nature of the gene—aside from the fact that nearly all genes hitherto studied behave like material particles existing in the chromosomes Nevertheless there is already evidence for a number of empirical principles regarding the changes of the genes, some of which may conveniently be listed here in the form of 14 statements I shall have opportunity merely to present these principles, without attempting any adequate explanations of how they have been derived from the data

1 The first and probably most important principle is that most genes—both mutant and normal —are exceedingly stable Some idea of the degree of this stability may be obtained from some quantitative studies of mutation which Altenburg and I have made in the fruit fly Drosophila It may be calculated from these experiments that a large proportion of the genes in Drosophila must have a stability which—at a minimum value—is comparable with that of radium atoms Radium atoms, it may be recalled, have a so-called "mean life of about two thousand years

2 Certain genes are however, vastly more mutable than others For example a gene causing variegation in corn, studied by Emerson and another in the four o clock, studied by Maryatt, ordinarily have a mean life of only a few years, and that causing bar eye in Drosophila has a mean life of only about 65 years as is shown by the results of Zeleny (In expressing these results we are here using the physicists' index of stability, which seems most appropriate for the present purpose also)

3 External agents do not ordinarily increase the mutability sufficiently (if at all) to cause an obvious ' production of mutation

4 The changes are not exclusively of the character of losses this is shown by the well established occurrence of reverse mutations in bar-eyed and white eyed Drosophila, in Blakeslee s dwarf Portulaca, Emerson s variegated corn, and probably in a number of other recorded instances It is known that mutations having an effect similar to that of losses do occur, however, and they may be relatively frequent

5 The change in a given gene is not in all cases in the same direction, and it does not even, in all cases, involve the same characters The latter point is illustrated by a series of mutations which I am investigating in Drosophila, which all involve one gene, but which produce, as the case may be, either a shortened wing, an eruption on the thorax, a lethal effect, or any combination of these three

6 The direction of mutation in a given gene is, however, preferential, occurring oftener in some directions than in others. This is well illustrated in the studies on variegated corn and four-o'clocks, and on the bar eye and white eye and other series in Drosophila

7 The mutability and preferential direction may themselves become changed through mutation, as illustrated by some of the same cases.

8 The mutations do not ordinarily occur in two or more different genes at once In only two instances in Drosophila have mutations been found in two different, separated[1] genes in the same line of cells of one individual. But a recurrent case apparently of this kind, has recently been described in oats, by Nillson Ehle

9 Not only does the mutation usually involve but one kind of gene—it usually involves but one gene of that kind in the cell. That is the allelomorphs mutate independently of one another, just as totally different genes do There is evidence for this derived from corn, Portulaca, and Drosophila

10 Mutations are not limited in their time of occurrence to any particular period of the life history This has been proved in the above mentioned studies on mutable plants, in Drosophila, and in other cases

11 Genes normal to the species tend to have more dominance than the mutant genes arising from them This is very markedly the case in Drosophila, where even the relatively few mutant genes that have been called dominant are very incompletely so, and might more justly be called recessive In other organisms, the same condition of things is *strongly suggested, although the direct data on occurrence of* mutations is as yet too meagre to allow of certainty

12 Most mutations are deleterious in their effects This applies not only to the organism as a whole but also to the development of any particular part the delicate mechanisms for producing characters are more likely to be upset than strengthened, so that mutations should more often result in apparent losses or retrogressions than in 'progressive' changes This is both an a priori expectation and a phenomenon generally observed

13 Mutations with slight effects are probably more frequent than those with more marked effects This must not be understood as referring to the different mutations of each given gene, but it applies in a comparison of the mutations occurring *in different genes.* Thus, there

[1] Contiguous genes may be affected in the rare cases known as "deficiencies" found by Bridges and Mohr

are more than a dozen mutations, in different loci, which reduce the size of the wing in Drosophila so slightly as to leave it more than half its original length, whereas only four reduce it to less than half length Mutant genes with effects so slight as to be visible only by the aid of specific co-genes seem to arise still more frequently It is reasonable to conclude that the mutations with slighter effects would more often take part in evolution, because they should usually be less deleterious and this conclusion is born out by observations on the multiplicity with which such factor differences with relatively slight effects are found in species crosses

14 The range of those mutations which are of appropriate magnitude to be visible is probably very small, in comparison with the entire "spectrum" of mutations, so that there are many more lethals than visible mutations, and probably more subliminal than visible

The above empirical and semi empirical principles must be regarded as a mere preliminary scaffolding, for the erection of a later more substantial, theory of mutation Time does not permit me here to discuss which directions of research, and what methods, seem the most promising for future results Suffice it to say that it is especially important to obtain accurate data concerning the effect of various conditions upon the rate of mutation This seems one of the logical routes by which to work towards the artificial production of mutation and consequent more perfect control of evolution At the same time such results should also give a further insight into the structure of the gene The way is now open, for the first time, to such studies on mutation rate, first through the finding, by Emerson, Baur, Maryatt, Zeleny, and Blakeslee, of a number of specially mutable factors in different organisms, and second, through certain special genetic methods which I have elaborated in Drosophila, for the detection of lethal and other mutations there

It has now become recognized that advances in theoretical or "pure" science eventually carry in their train changes in practice of the most far reaching nature—changes which are usually far more radical than those caused by progress in the applied science directly concerned It may therefore be asked at this point by eugenists "Are there any applications of the knowledge which has already been gained about mutation in general, to eugenics and to the principles which should govern us in guiding human reproduction?" I think that one such application is already clearly indicated

In order to understand the nature of this application it will be nec-

essary first to consider the proposition—emphasized by East and Jones in their book, "Inbreeding and Cross-breeding"—that the only way for a genetically sound stock to be formed is by its going through a course of inbreeding, with elimination, by natural or artificial selection, of the undesirable individuals that appear in the course of this inbreeding The truth of this proposition depends upon the fact that many recessive genes of undesirable character are apt to exist in a population Since the frequency with which these genes are able to produce their characteristic effects, i e, to "come to light," depends on *the closeness of the inbreeding, it is evident that inbreeding will be* necessary in order to recognize the genes adequately, and hence to eliminate them

Our present theory of mutation, however, carries us further than the proposition just considered It shows that these undesirable genes have arisen by mutation, in fact, as stated in point 12, the *great majority* of mutations are deleterious, probably even to the degree of being lethal, and it is also known, as noted in point 11, that many—probably the great majority—are recessive In other words, our mutation theory shows that probably the majority of the mutations that are occurring are giving rise to genes of just the type specified in the above discussion This immediately shows us that not only are inbreeding and selection desirable for raising the genetic level of a population, but they are absolutely necessary merely in order to maintain it at its present standard For the same process of mutation which was responsible for the origination of these undesirable genes in the past must be producing them now, and will continue to produce them in the future Therefore, without selection, or without the inbreeding that makes effective selection possible, these lethals and other undesirable genes will inevitably accumulate, until the germ plasm becomes so riddled through with defect that pure lines cannot be obtained, and progress through selection of desirable recessive traits can never more be effected, since each of them will have become tied up with a lethal To avoid such a complete and permanent collapse of the evolutionary process, it is accordingly necessary for man or nature to resort to a periodically repeated, although not continuous, series of inbreedings and selections in the case of any biparental organism

This conclusion is more than a mere speculation, or even a deduction from our principles The reality of this process of mutational deterioration has been directly proved, in the case of Drosophila, through experiments that I have conducted on lines in which the

processes that are essential for the effectiveness of inbreeding and selection were prevented in these lines there was found an accumulation of lethal genes so rapid that it would have taken but a few decades to have brought about the presence of a lethal gene in practically every chromosome of every fly Although the same general thesis undoubtedly applies also to mankind we do not yet know the speed of the process here Its speed depends upon the actual frequency of mutations, which it will be very important—and extremely difficult—to determine in the case of mankind Meanwhile, no matter what this rate may be, the process remains a real one, which must eventually be reckoned with, and either grappled in time, and conquered, or else yielded to

I have dwelt at length upon this particular application to eugenics, of some of the mutation studies I believe, however, that this is but one example of such applications, and that from an increasing knowledge of our theoretical science there will inevitably flow an increasingly adequate technique for coping with our refractory human material Meanwhile, the crying need is for more of the theoretical knowledge—and for the support of pure science, in its investigation of the processes lying at the root of the germ plasm

THE CAUSES OF MUTATIONS

In attempting to determine the causes of the appearance of new hereditary characters, we must first of all learn which of the categories of variation we are dealing with If we find that a so-called mutant has a different number or arrangement of chromosomes, we may say that this change in the chromosomes is the cause of the somatic differences seen in the mutant, for it would be strange if a relatively large change in the hereditary material did not affect the somatic expression of specific characters As has already been suggested by Gates, the cause of chromosomal aberrations may be environmental, as for example sudden lowering of temperature during critical periods of the germ cell cycle We have, however, no controlled experiments that prove this to be the case Again, there is a tendency to account for non-disjunction and other types of chromosomal aberration through purely internal causes, such as weakness of attraction between homologous chromosomes resulting in a failure of synapsis In general it may be said that, apart from being able to note a definite correlation between a changed somatic condition and a changed chromosomal

condition, we do not know very much about the causes of chromosomal mutations

The causes of gene mutations in *Drosophila* have remained, until recently, a complete mystery Muller had been able very slightly to increase the rate of mutation by raising the temperature of fly cultures, but he was not completely satisfied with these results In 1926, however, he startled the scientific world by the announcement that he had been able, by exposing adult animals to fairly heavy doses of X rays vastly to accelerate the rate of mutations Where some gene mutation occurred under normal conditions in only about 1 in 300 gametes, the X rays raised this ratio to 1 in 2 gametes, an increase of 150 per cent All of the old familiar mutations that had been occurring in untreated cultures were induced in much larger numbers by X rays but only a very few new mutations were produced It seems that the X-ray acts merely as a catalyst, hastening a process that would go on slowly without such an agent Numerous experimenters have followed Muller's lead in the use of X rays as an agent for accelerating the rate of mutations Muller has proposed a general theory that the ordinary, so-called "spontaneous," mutation of genes may be due to the presence of minute amounts of radio active substances accumulated in the tissues of plants and animals This theory seems somewhat far fetched at the present writing We are still in almost complete ignorance as to the causes of gene mutations and probably shall continue to be in ignorance until we gain some more accurate information as to the exact physical and chemical nature of genes and how they act in producing character differences

MUTATION AND EVOLUTION

T H MORGAN[1]

What bearing has the appearance of these new types of Drosophila on the theory of evolution may be asked The objection has been raised in fact that in the breeding work with Drosophila we are dealing with artificial and unnatural conditions It has been more than implied that the results obtained from the breeding pen, the seed pan, the flower pot and the milk bottle [used as breeding container for *Drosophila*] do not apply to evolution in the "open," nature "at large" or to "wild" types To be consistent, this same objection should be extended to the use of the spectroscope in the study of the evolution

[1] From *A Critique of the Theory of Evolution* Princeton University Press 1916

of the stars, to the use of the test tube and the balance by the chemist, and of the galvanometer by the physicist All these are unnatural instruments used to torture Nature's secrets from her I venture to think that the real antithesis is not between unnatural and natural treatment of Nature, but rather between controlled or verifiable data on the one hand, and unrestrained generalization on the other

If a systematist were asked whether these new races of Drosophila are comparable to wild species, he would not hesitate for a moment He would call them all one species If he were asked why, he would say, I think, "These races differ only in one or two striking points, while in a hundred other respects they are identical even to the minutest details' He would add, that as large a group of wild flies would show on the whole the reverse relations, *viz*, they would differ in nearly every detail and be identical in only a few points In all this I entirely agree with the systematist, for I do not think such a group of types differing by one character each, is comparable to most wild groups of species because the difference between wild species is due to a large number of such single differences The characters that have been accumulated in wild species are of significance in the maintenance of the species, or at least we are led to infer that even though the visible character we attend to may not itself be important, one at least of the other effects of the factors that represent these characters is significant It is, of course, hardly to be expected that *any* random change in as complex a mechanism as an insect would improve the mechanism, and as a matter of fact it is doubtful whether any of the mutant types so far discovered are better adapted to those conditions to which a fly of this structure and habitat is already adjusted But this is beside the mark, for modern genetics shows very positively that adaptive characters are inherited in exactly the same way as are those that are not adaptive, and I have already pointed out that we cannot study a single mutant factor without at the same time studying one of the factors responsible for normal characters, for the two together constitute the Mendelian pair

And, finally, I want to urge upon your attention another question Evolution of wild species appears to have taken place by modifying and improving bit by bit the structures and habits that the animal or plant already possessed We have seen that there are thirty mutant factors at least that have an influence on eye color, and it is probable that there are at least as many normal factors that are involved in the production of the red eye of the wild fly

Evolution from this point of view has consisted largely in introducing new factors that influence characters already present in the animal or plant

Such a view gives us a somewhat different picture of the process of evolution from the old idea of a ferocious struggle between individuals of a species with the survival of the fittest and the annihilation of the less fit Evolution assumes a more peaceful aspect. New and advantageous characters survive by incorporating themselves into the race, improving it and opening to it new opportunities In other words the emphasis may be placed less on the competition between the individuals of a species (because the destruction of the less fit does not *in itself* lead to anything that is new) than on the appearance of new characters and modifications of old characters that become incorporated in the species for on those depend the evolution of the race

CHAPTER XXVII

GUIDING FACTORS INTRODUCTION

Preliminary discussion —All of the factors hitherto discussed appear to operate on a random basis obedient to the laws of pure chance Of themselves then they might be conceived of as producing a high degree of diversity and innumerable novelties, but that would be all If there is something of orderliness, something of direction, something adaptive, something progressive, or even something purposive about evolution, there should be guiding factors responsible for each and all of them

The extent to which guiding factors are a necessary part of the evolutionary mechanism depends upon the extent to which there actually exist in nature conditions that cannot be accounted for on a purely random basis Guiding or directing factors imply goals objectives, definite trends improvements of one sort or another What is there about nature that seems to require a guiding hand?

Adaptations —One of the marvels of life is that the organism and the environment seem so well adapted to each other, that the particular organs of an individual seem so well designed to perform their many and varied functions that the various species are so nicely adjusted to one another in any given natural community that each seems to be a strand in an intricate and delicately adjusted "web of life" One of the most important goals or objectives of evolution, then, must be adaptation We are using these terms "goals" and "objectives" without implying any teleological considerations, though why there may not be purpose in nature I do not know At least it is better for the scientist to shy away from any taint of teleology So let us assume that adaptation is one of the main objectives of evolution using the term "objective" only to imply that evolutionary processes somehow, by devious paths, seem to arrive at various degrees of fitness The mechanism bringing about this fitness may be blind and may vision no goal but it gets there just the same

Since adaptation is so intimately associated with evolution—in fact, one of its principal attributes—it will be necessary to take a short excursion into natural history in order that we may come to realize at least some of the facts of adaptation that confront the evolutionist

and that challenge explanation The following chapter on "Adaptation in Nature" is frankly an interpolation but an essential one, unless the student be already well informed in this field Also the chapter on 'The Web of Life" is necessary if we are to avoid thinking of species as isolated entities The evolution of a species always takes place in a natural setting, part of which consists of the lifeless environment and part of which consists of its animal and plant neighbors

Orthogenetic trends —Various kinds of definitely directed evolutionary trends have been described Sometimes these trends concern themselves with such relatively trivial characters as the intricate markings on the shells of mollusks and brachiopods sometimes they have to do with the horns of elks or of titanotheres, and sometimes they concern the toes and teeth of the horse family One striking feature of these so-called "orthogenetic" series is that the trends have not always culminated in a condition of maximum efficiency but have sometimes gone beyond this point and have become positively detrimental in some cases even contributing to the extinction of the species possessing them If there is some guiding factor other than natural selection that tends to push evolutionary changes forward in definite paths such a force might be responsible for adaptive trends as well as the non adaptive ones In general however, it may be said in advance of the more detailed discussion of this question in a later chapter that most geneticists are either skeptical of the existence of any very definite orthogenesis, or else consider it explainable through natural selection

Progressive evolution —It is generally assumed that "evolution" and "progress are synonymous terms It is claimed that forms of life now living are on the whole more advanced than those that have lived in earlier times and that there has been a steady advance throughout the ages But what do we mean by progress in evolution or by more or less advanced forms? Progress and advance imply both direction and a goal or goals What are the goals toward which evolution is progressing?

Some claim that the final goal of life is perfect adaptation of all living things to the environment and to one another But is there any evidence that life today is any better adapted than was life in Cambrian times? Is there any ground for assuming that man is any better adapted to the environment than is the *Amoeba*? Man is adapted to a much more complex environment than is the *Amoeba*, but is he any better adapted to the human environment than is *Amoeba* to the amoeban environment? I see no reason for assuming that there is any difference

in the degree of perfection of adaptation in these two widely different species each highly successful in its own milieu and each cosmopolitan in distribution In view of such considerations as these, it is not easy to maintain that evolution is a process of becoming better and better adapted

Specialization —Various other criteria of progress have been suggested One of these is *specialization* Are the most highly specialized organisms more advanced than the less specialized? Are the more specialized ones closer to the ultimate ideal goal of evolution than the more generalized? Now, many of the most intensely specialized types of organisms are the parasites that have in many cases, undergone degeneration of sense organs locomotor structures, and even digestive systems but have developed specialized structures making it possible for them to live and thrive in some particular system of some species of host animal Here is specialization carried to extremes, but is it progress? I believe it is and for the following reasons

A primary objective of living organisms is that of exploiting to the fullest possible extent the energy resources of the world Ultimate success will be attained only when no further energy resources remain to be exploited Now the sources of energy are many and varied, and each different energy source requires a different type of energy-exploiting equipment Progress in specialization would therefore involve the evolution of as many highly specialized types of organisms as there are highly specialized energy sources Thus there is a very real value for life as a whole in the production of numerous highly specialized forms even though some be from the morphological viewpoint, degenerate and degraded parasites

Another type of specialization that has had a long and steady progressive evolution is the specialization of parts of the single organism for the performance of varied bodily functions This type of specialization is commonly called division of labor " In the course of animal evolution this specialization of parts begins at the lowest level in the Protozoa, where portions of the protoplasm are specialized to form organelles of various kinds each kind performing its own special function Among the lower Metazoa such as Coelenterata and Platyhelminthes, we have a new level of organization, built up of aggregates of units, each equivalent, in a sense, to a whole protozoan individual In these multicellular individuals division of labor is accomplished by specializing the cell units for different functions, with a corresponding increase in general efficiency of the individual

Among segmental organisms we have another advance in bodily specialization Here chains of individuals, each, in a sense, morphologically equivalent to a single individual of the flatworm type, become welded together into more complex segmented organisms With this new level of complexity of organization comes the possibility of specializing different segments, each of them equivalent to a whole individual of the lower grade, for particular functions Some perform chiefly nervous and sensory functions, others reproductive functions, and still others respiratory or digestive functions Each segment in certain parts of the body becomes a specialist in some one function which it performs more efficiently when relieved of some of the other functions Of course, specialization would be of no value unless integration and interdependence of part upon part kept pace with it Hence, one of the results of the trends just described is the closer integration of parts and the greater definiteness of individuality

Even among segmental organisms, as for example the ants and bees, division of labor takes place among segmental individuals and a new and higher level of organization—social organization—emerges Here in these insect societies, individuals are specialized in several ways some become functional males and females, others (immature females) become specialized as workers or protective units known as "soldiers" Thus, a society is, in a sense, a fairly definitely integrated individual of a higher level, involving a high degree of interdependence of the various kinds of specialists upon one another The integrating factor seems to be associated with the family relationship of all members of a given colony All members of a given colony are offspring of the same mother and father They are extremely clannish and resent vigorously any intrusion by outsiders

It therefore appears that one of the principal progressive trends of evolution is one in which units of lower orders are aggregated into complex units of higher orders Each aggregate is a new type of individual, with new properties not entirely the result of a summation of the properties of the ingredient units This idea has sometimes been spoken of as *emergent evolution* according to which, with each higher level of units, new properties of the whole emerge which are more than the sum of properties of the parts This might also be thought of as a kind of creation, for something new comes into being as though out of nothing

While the foregoing discussion is, in a sense, a digression, it seems well to call attention somewhere in a book on evolution to these facts

and theories The facts are there for us to explain, and the theories are attracting so much attention at present that they should not be ignored

Increase in size is one of the commonest trends of evolution, but is size increase progress? Many great groups of organisms have from age to age steadily increased in size of individuals Many fossil pedigrees show clearly that size increase is one of the steadiest of progressive trends But size if carried to extremes is disadvantageous, witness the complete extinction of the ancient dinosaurs and the rapidly progressing extinction of the whales and elephants today

Increase in intelligence is claimed to be one of the signs of progress in evolution In vertebrates, especially, there is a progressive series of forms showing greater and greater intelligence, ranging from fishes to man Accompanying and underlying this increase in intelligence, there has gone on in vertebrates a steady increase in the size, specialization, and compactness of the brain and its associated sense organs This steady trend is commonly spoken of by students of vertebrates as *cephalization* Is the final goal of evolution then the production of more and more intelligent organisms? If that were true, why should so much evolution be going on that seems to be moving in the opposite direction, resulting in the decephalization of many sedentary organisms and parasites?

You see it is difficult to discover any general or universal goal of evolution We do not even agree as to the direction of evolution, so we cannot be sure what is progress and what is regress Under these circumstances it may seem, at first thought, rather futile to discuss guiding factors at all Most of us, however, retain the firm conviction that evolutionary change has in it something of direction, something of fitness, and something of progress, though we may not always be able to demonstrate direction or fitness or progress in particular cases

Evolutionists, however, have always assumed that evolution is progressive, that adaptation is a reality, and that there have been definite evolutionary trends Believing in these phenomena, they have tried to explain them The two classic attempts to explain progressive evolution are Darwin's theory of natural selection and Lamarck's theory of the inheritance of acquired characters These theories are to be critically discussed in chapters xxx and xxxi respectively

CHAPTER XXVIII

ADAPTATION IN NATURE

THE NATURE OF ADAPTATIONS

"The adaptation of every species of animal and plant to its environment," says Jordan and Kellogg,[1] "is a matter of everyday observation So perfect is this adaptation in its details that its main facts tend to escape our notice The animal is fitted to the air it breathes, the water it drinks, the food it finds, the climate it endures the region which it inhabits All its organs are fitted to its functions all its functions to its environment Organs and functions are alike spoken of in a half figurative way as concessions to environment And all structures and powers are in this sense concessions, in another sense, adaptations As the loaf is fitted to the pan, or the river to its bed, so is each species fitted to its surroundings If it were not so fitted, it would not live But such fitness on the vital side leaves large room for variety in characters not essential to the life of the animal '

The authors quoted above appreciate what is perhaps the most significant fact about adaptations that the adaptations are to a large extent molded by the environment and therefore fit the environment So long as the environment remains uniform, a given species will remain unchanged, except for minor fluctuations and occasional mutations, but if the environment changes, sometimes even slightly, the development of the individual responds in such a way as to give a radically different end product So we may conclude that a large part of the fitness of the organism to the environment is due to the fact that the development of each individual is molded by the environment so as to fit it Thus some at least of the apparent mystery of adaptations is dispelled

When we think of the fitness of the organism to the environment we take an entirely one-sided view of the matter, for if the organism fits the environment, no less certainly must the environment fit the organism This idea of the "fitness of the environment" has been

[1] From D S Jordan and V L Kellogg *Evolution and Animal Life*

admirably discussed by Professor Lawrence J Henderson in a stimulating volume[1]

Henderson points out that the environment, no less than organisms, has had an evolution. The particular environmental complex as it exists today is absolutely unique There is hardly an element of the effective environment that could be changed without causing the extinction of life or at least a transformation of it so profound that it might not be life at all as we know life Water, for example, has a dozen unique properties that condition life Carbon dioxide could not be replaced by any other substance The properties of the ocean are so beautifully adjusted to life that we marvel at the exactness of its fitness Finally, the chemical properties of carbon, hydrogen, and oxygen, the most abundant elements, are equally unique and unreplaceable In brief given the environment as it is, life could not be other than it is The evolution of the environment and the evolution of organisms have gone hand in hand, or perhaps we might better say hand in glove, for this better expresses the idea of mutual fitness

Within the realm of the general environment as conceived by Henderson there are almost innumerable special environments due to particular combinations of the various environmental units Within the aquatic environment, for example, there are variations such as differences in salinity, varying from extreme saltiness to almost total lack of salt, there are inshore conditions and open sea conditions, there are surface conditions and those at relatively great depths, and there are great differences due to temperature Similarly on land, there are surface conditions, subterranean conditions, arctic, tropical conditions, caves, deserts, forests, plains, mountains, and many others No two areas on land are precisely similar in all respects All of this makes for a corresponding multiplicity of animal and plant forms In the case of plants the action of the environment is remarkably direct, for the plant cannot get away from a fixed environment If the environment undergoes material change, the plant's only response is a structural one For example, if plants that are accustomed to a relatively humid climate are grown in the desert they develop numerous xerophytic adaptations such as small leaves with greatly diminished transpiration surface, a thick epidermis, hairs, or spines, small stature, deep-root system, and other similar protections against the inimical desert conditions Similarly, plants accustomed to grow in relatively

[1] L. J Henderson *The Fitness of the Environment* 1913

dry soil, if grown in soil that is covered over with water, will produce aquatic leaves and roots and undergo appropriate changes in epidermis and loss of supporting tissues, for plants that are buoyed up by water need little support

Animals, on the other hand, are for the most part not so intimately related to a local environment as are plants They are characteristically mobile creatures with varying capacities for wandering about and selecting the habitat that best suits them

"By virtue of being unlike or possessing different properties," says Shelford,[1] "the various animal species require different conditions for the best adjustment of their internal processes For example, the carp lives in shallow and muddy ponds and rivers, while the brook trout lives only in clear swift streams These two organisms are able to move about and find places to which they are suited The differences between them are clearly indicated by the differences in the habitats which they prefer

"By observation and by experimentation it has been shown that animals select their habitats By this we do not mean that the animal reasons, but that selection results from regulating behavior The animal usually tries a number of situations as the result of *random movements*, and stays in the set of conditions in which its physiological processes are least interfered with This process is called selection by trial and error If animals are placed in situations where a number of conditions are equally available, they will almost always be found living in or staying most of the time in one of the places The only reason to be assigned for this unequal or local distribution of the animals is that they are not in physiological equilibrium in all the places However, some animals move about so much that it is with some difficulty that we determine what their true habitats are"

This idea of habitat preference and habitat selection is extremely important for a correct understanding of adaptation or the fitness of organisms to environments Much of the observed fitness may be due to the fact that an organism has chosen out of a wide range of environments the one that best suits it We cannot in such a case say that the environment has had a direct influence in shaping the organism any more than we could say that, when a man tries on various shoes and finds a pair to fit he has been responsible for the fitness of the shoes

Many special adaptations may be explained through habitat choice. Thus animals such as the duckbill platypus, the lung fishes,

[1] V E. Shelford, *Animal Communities in Temperate America* (1913)

and others whose teeth are replaced by bony or chitinous plates that are used for crushing the hard shells of molluscs and crustaceans, may not confidently be said to have developed these crushing appliances and to have abandoned the use of teeth in adaptation to a habit of feeding upon hard shelled prey, but rather it seems more likely that the loss of teeth and the development of crushers occurred through a degenerative process incident to racial senescence and that the possession of the crushing equipment enabled them to avail themselves of a new type of food formerly unavailable to them

The organic environment—In his admirable chapter entitled The Web of Life, ' which we shall quote entire Professor Thomson has given us a vivid picture of vast systems of interdependencies that exist throughout the organic world No species, no creature, lives to itself alone it is intimately tied up with a host of other creatures with interwoven destinies Thus one species of animal is adapted to live upon certain plants or other animals which in turn may be dependent upon still other animals or plants The elimination of one species may cause the elimination or the radical change of a dependent species We cannot afford ever to forget this great truth of the oneness of nature It is the keynote of life and of evolution

Adaptation due partly to functional activity —It is a commonplace which needs no special demonstration to say that organs improve through use and deteriorate through disuse Many organs then, which in the adult condition appear to us to be so admirably adapted to perform certain duties, must be thought of as having been gradually molded by functioning during the entire period of individual development If the motor nerve running to a limb bud of a growing embryo be severed at an early stage and no secondary nerve connection be established, the limb will continue to grow up to a certain point, but in its paralyzed condition will be incapable of exercising its functions and will cease to develop A certain amount of development will therefore be seen to be independent of functioning but full development of functional efficiency is obtained only through functioning

"The relation between structure and function in an organism says Professor Child,[1] ' is similar in character to the relation between the river as an energetic process and its banks and channel From the moment that the river began to produce structural configurations in its environment, the products of its activity accumulated in certain

[1] C. M Child "Regulatory Processes in Organisms *Jour Morph* Vol XXII (1911)

places and modified its flow It moulds its banks and bottom forming here a bar, there an island, here a bay, there a point of land but still flowing on though its course its speed, its depth the character of the substances which its carries in suspension or in solution, all are altered, built up by its own past activity " According to this view, structure is simply the resultant of the interaction of function and en vironment or of functional activity Though perhaps a little extreme for most of us, this view is we believe essentially correct. We are prone to overemphasize structure in our discussions of adaptation and evolution and to lay too little stress upon the energy side of development Certainly no structure is ever formed without protoplasmic activity of a very definite sort and in this sense adaptations are to be thought of as the results of functioning Why, then, do we claim to be astonished at the effective way in which certain organs accomplish their functions, when functioning has taught them their task?

TWO CATEGORIES OF ADAPTATIONS

There are, according to E G Conklin two categories of adapta tions (a) racial or inherited adaptations and (b) individual, acquired or contingent adaptations All of the direct molding effects of environ ment or of developmental functioning together with adaptative rela

for they concern themselves with individuals, not with races The adaptive condition is simply made over afresh in each generation and the only thing that seems to extend beyond the immediate individual or generation is a general plasticity or responsiveness of the specific protoplasm which enables it to adjust itself to special life conditions There is nothing mysterious or baffling about this situation, for it in volves merely a repetition of certain appropriate responses by each individual It is a problem of individual development, not of racial *development or evolution*

Inherited Adaptations —There is, however, a large category of adaptations which appear in the organism as though in anticipation of the rôle they are to play some time in the future and not in response to any present need In this category are the eyes, the lungs, the vocal organs, the taste buds, and many other organs of the human fetus

Thus the eyes of the new born infant are essentially finished mechanisms before they ever function as organs of vision They cannot therefore have been molded for their visual function by functioning in a visual manner Of course they must have been functioning in some way, as all living protoplasm must function, but they cannot have functioned in a way that would in itself account for the fact that the eye is a very intricate optic mechanism Similarly, the human infant has good lungs and good vocal cords before it ever takes the first breath of air or gives the first cry Such adaptive structures as these are said to be *racial* or *inherited adaptations* Any theory of evolution worthy of the name must account for the origin and perpetuation of such inborn adaptations It was partly to explain the origin and perfection of adaptations such as these that Lamarck proposed his theory of the *inheritance of acquired characters* and Charles Darwin devised his theory of *natural selection* It is still unsettled as to which of these theories is the more adequate, but the consensus of expert opinion favors Darwin s explanation

It would be impossible to give any comprehensive account of animal or of plant adaptations in the brief space of such a chapter as this Let it suffice to classify adaptations and to describe a few representative adaptations confining our attention to those which are obviously racial or inherited in character

ADAPTATIONS CLASSIFIED

Adaptations are variously classified by different authors, and that of Jordan and Kellogg is as good as any "(*a*) food securing (*b*) self defense, (*c*) defense of young (*d*) rivalry (*e*) adjustment to surroundings

Some very common adaptations may belong to several of these categories at once Thus the sharp teeth and hooked claws of carnivorous mammals serve equally well for food securing, for self defense, for defense of young, and for rivalry Similarly, the horns of deer and other ungulates are equally adapted for self defense, defense of young and rivalry

There can be no especial advantage, in this connection, in presenting a detailed review of adaptations of the sorts given in the foregoing classification, therefore we shall confine our efforts to a description of a few typical adaptations about which the greatest controversy has raged

SOME SPECIAL ADAPTATIONS

The electric organ of the torpedo, a widely distributed elasmobranch fish, consists of a sort of honeycomb like structure on each side of the head This structure acts as a storage battery and is capable of storing up electricity of considerable voltage The animal is capable of giving a very distinct shock to an attacker and can thus defend itself quite effectively There is also an electric eel, native to the waters of Paraguay and Brazil, that is able to give severe shocks to bathers or to horses driven through the streams A type of catfish native to the river Nile has a similar electric equipment In all of these cases the storage battery is made up of modified voluntary muscles and is of considerable size

The mammary glands of mammals are skin glands usually with well-defined ducts leading to the surface and terminating in teats These glands are quite voluminous and serve admirably the purpose of feeding new born young until the latter are able to use the more varied food normal to the adult. In the lowest mammals the monotremes or egg laying mammals, these glands are relatively poorly developed and diffuse, also they are known to be developed through a regional specialization of sweat glands. In the true mammals or Eutheria the glands are modified sebaceous or oil glands and may be seen to develop from the same embryonic rudiments as the latter

The marsupial pouch of the kangaroo and its allies is a pocket like fold of the integument, folded forward or backward over the region of the abdomen in which are located the mammary glands This pouch is used as a shelter for the tiny immature larval foetuses Hartmann has recently described a very striking piece of behavior in connection with the birth of young opossums The young are born in an exceedingly immature state and looking like tiny pink grubs They crawl under their own power, by means of a swimming like motion, through the hairs of the mother's abdomen, till they reach the pouch This they enter unaided and each tiny larva finds for itself a slender tubular teat, which it swallows and holds in place by a specially adapted hold fast mouth The young remains attached fixedly to this teat for some weeks, feeding almost constantly on milk After a long interval the teat is released, the mouth metamorphoses into the adult form and the young feeds only at intervals as do the young of other mammals This complex of adaptive structures and instincts is among the most remarkable in the annals of biology

The fetal membranes of higher mammals constitute one of the most efficient adaptive complexes known. Surrounding the embryo is a fluid filled sack (amnion) which furnishes an aquatic environment for the soft and delicate body, preventing harmful contacts and allowing ample free space for expansion. The placenta is a co-operative structure, developed out of both fetal and maternal materials, that furnishes an excellent medium for nutritive and other metabolic exchanges between mother and fetus. Although there is no direct vascular connection between them, the mother gives of her nutritive materials to the fetus and takes up from the fetus and eliminates its wastes. As an adaptation for carrying out an intricate set of physiological exchanges between two otherwise entirely separate individuals the placenta is unexcelled.

Nest-making instincts in birds represent, on the behavior side adaptations of extraordinary perfection. Some nests are built with the greatest care and precision, others represent a relatively crude and slovenly performance. Some nests are made of twigs, fibres, and mud, others of mud alone, still others are hollowed out in clay or sand banks, and some are made in holes in the ground. In any case, the type of nest is highly specific and due to a hereditary instinct, for birds receive no instruction in nest making.

Before bringing to a close this brief list of particularly noteworthy adaptations let us recall to mind the series of special adaptations listed as examples of the laws of adaptation, such as aquatic, arboreal, cursorial, flying, burrowing, ant eating, and, especially, adaptations of deep-sea animals.

PARASITISM AND DEGENERATION

A vast number of animals and plants have given up the active search for food and have taken up the relatively easy habits of parasitism. In adaptation to this life certain structures have developed and many of the characters found in independent, free-roving creatures have disappeared or become reduced to mere vestiges. Thus the more completely dependent or parasitic an animal becomes, the more completely does it lose its organs of locomotion and its sense organs such as eyes, auditory organs, tentacles, etc. Some animals are free living when young or in the larval condition and only settle down to a parasitic life when near the end of the life-cycle, other animals are parasitic only when young or larval and become independent in the adult condition, still others are parasitic throughout the entire life-cycle and pass from host to host without any interval of independent life. Some of these complete parasites pass one phase of the life-cycle on one species of host and the remainder on another

species of host. Thus the liver fluke in the adult condition lives in the gall bladder of the sheep, while the early larvae live within the body cavities of a species of land snail The transfer from host to host in this case must be a procedure involving many chances of failure to a very few chances of success, and, in adaptation to these vicissitudes the number of eggs and larvae produced by a single adult individual runs up into the millions

The classic case of extreme parasitic degeneration is that of *Sacculina* The young larva of *Sacculina* is a typical entomostracan crustacean larva which swims about and leads a free life for a time but soon attaches itself by means of its antennae to a hair pit of a crab a small hole in the latter's armor The internal tissues of the larva then undergo degenerative processes and are reduced to an almost fluid mass of embryonic cells, which flow through the hair pore of the crab, and into the latter's lymph spaces The small mass of cells then rounds up and is carried about with the circulation of the crab s blood until it comes to a favorable place of lodgment, usually the wall of the intestine just back of the stomach. Here it flattens out and sends rootlike branches almost all over the crab s body, like a malignant tumor in its invasion of foreign tissues The unbranched part of the parasite is little more than a sac of reproductive organs, and these produce eggs and sperms, which unite to produce larvae By this time the host is killed and with the decay of its body, the larvae escape into the sea water ready for a brief period of free life before attacking another host

Almost every group of animals and most of the groups of plants have their parasitic representatives and every degree of parasitism and the accompanying degenerative changes are to be found. Of course, it is an open question whether parasitism causes degeneration or whether degenerating creatures take refuge in parasitism but in either case the adaptive features of the situation are obvious

Commensalism —If parasitism be defined as an association between two organisms in which one (the parasite) lives at the expense of and to the detriment of the other (the host) commensalism may be defined as an association in which the two organisms exist in close association without any positive detriment to either In some cases the claim is made that the association is mutually beneficial but as a rule the relation is relatively one-sided.

An interesting example of commensalism is that of the sea cucumber and the little fish *Fierasfer* This strange little animal inhabits

the rectum of the sea cucumber and may be seen to lie with only its head out From this shelter it darts forth to capture its prey, which done, it returns to its shelter Curiously enough the vent of the little fish is situated just back of its mouth so that its wastes may be voided when in its usual position There can be no advantage to the sea cucumber in such an arrangement, though no particular harm is done Another case of this sort is that of several species of Remora which attach themselves by a large diskoid adaptation on top of the head to various fish such as sharks, barracudas, etc

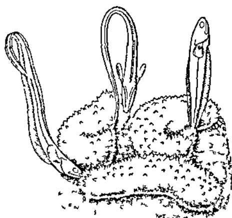


Fig 78 —*Fierasfer acus* penetrating the anal openings of holothurians ⅚ natural size (*From Boulenger after Emery*)

The sucking disk is a modified dorsal fin The remora merely gains free transportation to more favorable feeding grounds When the desired food is sighted the passenger leaves its conveyance temporarily, but returns by a sudden swift dash and resumes its hold The shark gets nothing except perhaps the sense of companionship, and is also undoubtedly somewhat hindered in its locomotion

Some of the most remarkable cases of commensalism are found in connection with elaborate colonies of ants In some cases two species of ants live together in the relationship of masters and slaves The master species is unable to perform any of the ordinary duties of the colony, such as securing food, taking care of young, etc In extreme cases the masters are only soldiers, specialized for fighting and marauding, and cannot even feed themselves unaided The slave species would be able to carry on to some extent if not captured, but thrives exceptionally well under the protection of the soldier species There are among ants many varieties of commensal relationship less extreme than this, but this will serve as a typical case

Communal life —Among the higher insects and higher vertebrates, especially among the ants and bees, we find a very elaborate social life In ants, for example, the typical colony consists of a queen (the only fertile female in the colony), several males (mates of the queen),

ordinary workers (sterile females of the first type), soldiers (sterile females of the second type), and sometimes officers (especially large and powerful sterile females that seem to direct the line of march in legionary ants) All of these casts are produced from the eggs of one female and are the result of various special diets permitted the larvae by the workers Among bees, similarly, there is one queen, a number of drones (males), and the sterile female workers, who perform the functions of nursing the larvae, cleaning up the hive, collecting pollen and nectar, and making honey and wax Detailed accounts of the lives of bees have been given by various authors, notably by Maeterlinck in his *Life of the Bee*

ADAPTATIONS OF DEEP SEA ANIMALS AND OF CAVE ANIMALS

One of the weirdest environments the world affords is the bottom of the sea at great depths There it is dark and cold and almost devoid of oxygen, while the pressure is almost unbelievably high Yet in these vast and forbidding abysses there dwell in apparent comfort representatives of most of the animal phyla Fishes of many sorts, crabs mollusks, worms, and many other forms thrive and multiply in this seemingly cheerless environment We do not at all understand the nature of the adaptive mechanism that enables these animals to withstand with their frail bodies the steel crushing pressures that prevail at all such depths We do know, however, how some of the deficiencies of the environment are made good by these denizens of the deep Thus many abysmal forms produce their own light by means of phosphorescent organs placed at advantageous points of their bodies Not only fishes of the depths, but some mollusks possess forms of artificial lighting equipment One species of cephalopod (related to the octopus) is described by Wiesmann as bordered with twenty large phosphorescent lanterns that present the aspect of a display of variegated gems, colored ultramarine, ruby red, sky blue, and silvery white

Equally highly adapted to life in a world of darkness, the monotony of which is broken only by the occasional spots of light emanating from the various living lanterns just referred to, are the strange eyes of some of the abysmal fishes Sometimes these eyes are enormously large, and thus adapted to bring to the perception of the animal the weak light of the depths, or again they may be modified still further in a strikingly peculiar manner, each being drawn out into a cylinder [illegible] of the head like a telescope Such [illegible]

and making the environment visible Could man view the sea bottom through some of these instruments, he would doubtless add something very novel and weird to his scenic repertoire

Other creatures of the darkness live strange lives in caves such as the Mammoth Cave of Kentucky Most cave dwellers are blind or nearly so and usually have a pale and ghostlike appearance because of their lack of pigment All grades of defective eyes are found, ranging from those that are merely somewhat smaller than normal to those that remain deeply imbedded in the head in a relatively undifferentiated state It goes without saying that such animals are better adapted to life in caves than they would be outside One pressing problem of biology is How did the cave animals become blind? Did they wander into the caves as normal animals and become blind because their eyes were disused, or did they become blind outside through no fault of their own, as the result of a mutation, and by chance find safety in an underground stream or a cave? The first explanation is Lamarckian, the second Darwinian

COLOR AND PATTERN IN ANIMALS

"The phenomena of color in both animals and plants," says Metcalf,[1] "are among the most remarkable and interesting in the whole realm of nature It is not so much the way in which the color is produced whether by pigments or by refraction that interests us in this connection as it is the uses to which colors are put Let us first refer to the colors of animals

"According to the uses to which colors in animals are put, we may classify them, for purposes of description, as follows

"Indifferent coloration, not useful, so far as we can judge,
Colors of direct physiological value,
Protective coloration and resemblances,
Aggressive coloration and resemblances,
Alluring coloration and resemblances,
Warning coloration,
Immunity coloration
Mimetic coloration and resemblances,
A Protective
B Aggressive
Signals and recognition marks,
Confusing coloration,
Sexual coloration"

[1] M M Metcalf, *Organic Evolution* (1911)

Much has been written about these various categories of animal coloration nearly all of which assumes some special adaptive value for each type of color or pattern

The above classification is typical of the older views as to animal coloration in that it recognizes no colors as merely incidental by products of metabolism, but assumes that all colors are valuable as adaptations Modern critics are inclined to consider that at least many colors are to be explained as the result of the fact that certain chemical materials are formed in the elaboration of tissues and in the physiological processes that must go on in these tissues, which, because of their light absorptive properties, appear to our eyes as colored The color may chance to enhance the protective resemblance of the animal or it may make it more conspicuous than it should be in either case it may have an incidental value But colors may come and colors may go irrespective of adaptive value, for many colors are so placed in the organism that they can never be visible and color is only in the seeing While we have no intention of denying the adaptive value of animal colors, it seems wise to get away from the extreme anthropomorphic interpretation of these colors, for some of the categories of coloration listed in the previous paragraph are largely, if not wholly anthropomorphic It has been the habit of students of coloration to assume that insects, birds, lizards and other animals see colors and patterns as man sees them that what is attractive to man must also be attractive to the lower animals that what is confusing to man would

takes no notice of colors at least when they are at rest, but will jump at any moving object of about the right size

Modern students are inclined to think that many of the minor categories of animal coloration listed above are at best, of very questionable significance and that practically all categories simmer down to one *obliterative coloration or camouflage*

"All naturalists,' says G H Thayer[1] perceive the wonderful perfection of the twig mimicry by an inchworm or of bark by a moth or of a dead leaf by the Kallima butterfly It is now apparent that almost equally marvelous concealment-devices in one shape or another are general throughout the animal kingdom *the most gorgeous*

[1] G H. Thayer *Concealing Coloration in the Animal Kingdom* The Macmillan Company 1918

costumes being, in their own way, climaxes of obliterative coloration scarcely surpassed even by moths or by inchworms

"This discovery that patterns and utmost contrasts of color (not to speak of *appendages*) on animals make *wholly* for their 'obliteration,' is a fatal blow to the various theories that these patterns exist *mainly* as nuptial dress, warning colors, mimicry devices (i e , mimicry of one species by another), etc , since these are all attempts to explain an entirely false conception that such patterns make their wearers *conspicuous* So immeasurably great, in the case of most animals, must be the value of inconspicuousness that such devices as achieve this to the utmost imaginable degree, upon almost every living creature, demand no further reason for being (although doubtless serving countless minor purposes) Apparently, not one 'mimicry' mark, nor one 'warning color' or 'banner mark' nor one of Gadow's light and shadow begotten marks, nor any 'sexually selected color, exists anywhere in the world where there is not every reason to believe it is the very best conceivable device for the *concealment* of its wearer, either throughout the main part of this wearer s life, or under certain peculiarly important circumstances The so-called 'nuptial' costumes of animals are demonstrably an increase of such potency of obliterative coloration as belongs to all gorgeously varied costumes, *and this at the very period when concealment is most needed* "

Thayer believes 'that the colors, patterns, and appendages of animals are the most perfect imaginable effacers under the very circumstances wherein such effacement would most serve the wearer Many animals when observed in a museum show case or in a menagerie, appear to us to be most conspicuous but the elements that lend conspicuousness in the artificial environment may be the very ones that tend to efface the wearer when in his native haunts The most brilliant birds, such as mandarin ducks, birds of paradise, flamingoes peacocks, parrots, etc , are shown to be almost invisible in their natural surroundings

The schemes for producing obliterative protection are much the same as those made use of during the recent war The simplest scheme of all is that of having the same color and pattern as the background Thus many green insects, amphibia, reptiles, birds, and a few mammals that live in trees, smaller plants, or grass, are colored green Many desert animals are sand colored Many marine animals living near the surface are transparent or nearly so Another scheme is known as *counter shading*, according to which most animals with little variety

of color are concealed by having the upper surfaces dark, the lower surfaces light, and a blending of one into the other on the sides Nearly all birds of the open, such as sea birds and soaring birds, use this method of concealment The same is true for fishes that live near the surface, and for many mammals that are likely to be seen against a sky line Actual demonstrations have shown that this method of concealment is highly effective, no matter from what point of view the animal may be seen A third scheme is one that was used most effectively during the war in concealing battleships, heavy artillery, and other large objects, namely, destroying the continuity of outline by using large, irregular patches of contrasting or light and dark colors In this way a broken, irregular patchwork of color takes the place of a coherent, regular contour It is probably in this way that many of the most brilliant coral reef fishes attain concealment. Instead of the fish as a whole being the center of vision, the bright patches stand out against the dark, and these fail to give any picture likely to be interpreted as a fish either by enemies or by prey Professor Reighard interpreted the brilliant patterns of reef fishes as examples of ' immunity coloration,' the idea being that these fishes were so safe from attack and so little in need of concealment from prey that they simply went the limit in color display, unchecked by natural selection Longley has recently shown that the patterns and colors of such fishes are in reality obliterative, and if this be true, there is no need of introducing the idea of ' immunity coloration "

In view of the above considerations, it now seems likely that essentially all types of animal coloration that have any adaptive value at all —and by no means all have any demonstrable adaptive significance—may be classed under the general head of concealing coloration, and if this be so it greatly simplifies the problem of the evolutionist Much of the controversy as to the efficacy of natural selection has been waged about some of the questionable categories of animal coloration, such as warning coloration," "mimicry, ' "confusing coloration," "sexual coloration ' If all of these turn out to be merely phases of concealment coloration, their origin could be explained as readily as that of any other adaptive character of definite selective value

The Case of Kallima —With this general introduction to the subject of animal coloration, it does not seem necessary to list examples of all the categories of color mentioned Let us close the discussion with what appears to be the classic instance in biological literature of perfect protective resemblance that of the "dead leaf butterfly," *Kallima* (Fig 79)

"Its wings, says Herbert, "when upturned, represent on their underside a perfect copy of a leaf with a midrib and a regular succession of side veinings Differently colored spots on the wing imitate patches of decay and mildew, while the prolonged tail of the hindwing, which touches the stem in the sitting posture of the butterfly,

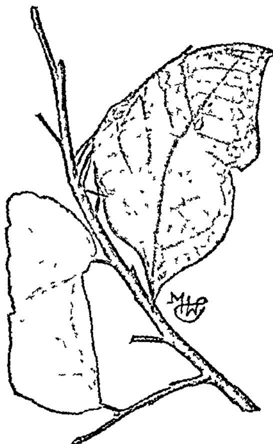


Fig 9—*Kallima* the dead leaf butterfly (*From Jordan and Kellogg*)

makes it appear as though the leaf was directly growing out of the stem It is only when at rest upon the stem of a tree that the resemblance to a leaf would be effective, for it is only the under surfaces of the wings that are protectively colored The upper surfaces of the wings are brightly colored and would supposedly be quite conspicuous when the insect is in flight " These insects," says Metcalf, "are very noticeable when in flight, but when they light and close the wings, their

sudden disappearance is most startling and confusing greatly increasing the difficulty of observing their resting place" According to this idea of 'confusing coloration," a butterfly is supposed to mystify or confuse its enemies by first attracting their attention and then suddenly becoming invisible *One is reminded of the prestidigitator of his* favorite remark "Now you see it and now you don t' But why attract attention in the first place when continued inconspicuousness would be much less risky? The best answer to this question is to use Thayer's interpretation, namely, that what looks like a conspicuous coloration when observed in the stationary insect held against an alien background is probably almost invisible when the animal is moving its wings and flying through the air in the bright sunlight

The case of *Kallima* is probably more or less typical of the somewhat uncritical tendency on the part of naturalists to invent adaptive explanations for every striking color or pattern seen among animals Let us examine the situation a little further Much has been said about the minute details of resemblance to a dead and decaying leaf on the part of this butterfly, yet, if its habits are at all like those of other members of its order, it is hardly likely that its most active period would coincide with that in which the leaves of trees would be decayed *and mildewed or even brown Butterflies are active when flowers,* whose nectar forms their chief food, are numerous and are usually in their pupa cases when the leaves have died on the trees It has also been stated by critical observers that *Kallimas* do not frequently light on trees whose leaves are very similar in shape to the folded wings of a butterfly Furthermore, there are many kinds of butterflies that are more or less like leaves, in fact, it would be difficult for a butterfly not to look somewhat like a leaf, since the wings are shaped like leaves Again, many species of butterflies have the swallowtails on the lower wings without in other ways much resembling a leaf others have spots that might be interpreted as resembling decay and mildew without in other ways being more than in general leaflike, and there are many other species that show all degrees of leaf resemblance, some very imperfect and others almost as perfect as that of *Kallima*, yet they all seem to be essentially successful in the life-struggle in spite of their less perfect protective resemblance

Alleged cases of mimicry have failed also to meet critical examination When a poisonous butterfly is mimicked by an edible species several conditions must be met in order that the deception be effective The model and the mimic must both occupy the same range,

have the same period of activity and the same general habits The model must be much more numerous than the mimic *Unfortunately* for the proponents of mimicry, it has sometimes been found that several of these requirements are lacking Attempts to explain away the discrepancies have been far from satisfactory

All these considerations should make us cautious about reading into the colors and patterns of animals too many adaptive details It is more than likely that the majority, if not all, of these apparently marvelously exact instances of imitative resemblance would turn out, when critically examined, to be no more nor less adaptive in special ways than is *Kallima* and the mimics

One lesson that the naturalist may well learn from the present discussion is this There is enough in the way of adaptations for the evolutionist to explain without burdening him with hypothetical or interpretative adaptations First find and prove your adaptation, *then try to explain it Don t explain it first and then find out* later that it was not so much of an adaptation after all

OSBORN'S LAWS OF ADAPTATION

Adaptations have been variously classified by different writers Perhaps the most significant classification is that of Osborn which is based on their supposed evolutionary origin According to this writer and others, there are two categories of adaptations to environmental conditions *the first has to do with the tendency of unrelated* species to assume similar structures under similar environmental conditions, the second has to do with the tendency of related species to assume different adaptive structures under different environmental conditions In both categories the environment appears to be the determining factor

(1) A good example of the first category, which illustrates what Osborn calls "the law of convergence or parallelism of form," is seen in the tendency of many aquatic types of vertebrates to assume the fishlike form As is well shown in Fig 80 the shark (a fish) the ichthyosaur (an extinct aquatic reptile), and the porpoise (a marine mammal), all possess the same fusiform body best adapted for speed under water, the same types of locomotor structures consisting of the great propeller fin (caudal fin) and the steering and balancing fins, the dorsal fins and paired fins Apart from these superficial adaptations for swift locomotion in the water, the three types are profoundly different The shark breathes with gills, the reptile and mammal with lungs, the fish and reptile are cold blooded, the

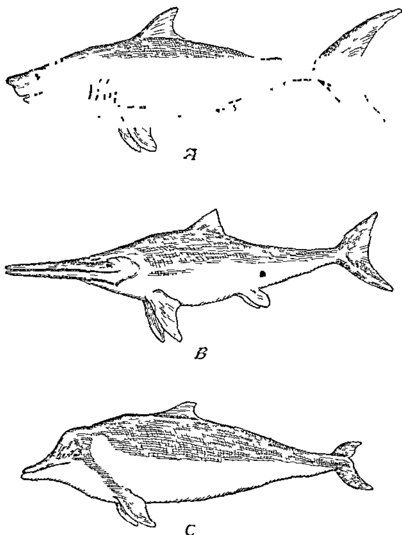


Fig 80 — Three aquatic types of vertebrate, to illustrate convergent adaptation of three wholly unrelated forms of marine life All three show the fusiform body, median and paired fins, though the skeletal structures are radically different *A*, shark (Pisces), *B* ichthyosaur (Reptilia), *C*, porpoise (Mammalia) (*From Newman after Osborn*)

mammal warm blooded The internal anatomy of the three differs fundamentally in every detail

A list of other types of convergence will more adequately illustrate the law

Flying and parachuting animals occur among nearly all vertebrate and some invertebrate classes Planes of some sort are found for supporting the body in the air The plane is made in various ways in different groups but functions much the same in all of them

Running animals of various classes have long legs, and a tendency to stand on the toes There is also in several unrelated groups the tendency to reduce the number of toes, the culmination of which is seen in the one-toed horses

Climbing animals are all provided with clinging appendages of some sort, including such structures as hooked claws, prehensile fingers or tail, suction pads on the feet, and other similar adaptations

Burrowing animals have as a rule, extra heavy shoulder girdle and strong fore limbs with heavy gouging claws Many of them also are blind or nearly so as befits life in dark underground passages

Desert-dwelling animals as a rule are provided with heavy scales spines or armor, to prevent excessive loss of moisture and as a protection against spiny plants They also usually have burrowing habits enabling them to escape the extremes of heat and cold

Cave animals are usually blind or nearly so and are relatively pale in color, sometimes without any pigmentation

Deep-sea animals of many sorts have phosphorescent organs by means of which they either attract their prey or find their way about the dark sea floor Some of these organs, called "lanterns,' can be used as searchlights The eyes of deep-sea fish are either enormously large or are "telescope eyes," adapted for sensing light of low intensities

Ant eating animals, belonging to several distinct groups, are heavily armored against the attacks of ants, have strong claws for digging up ant galleries, have long snouts or beaks with a long sticky tongue for capturing ants and an arrangement of the glottis to prevent ants from crawling into the lungs

2 There are almost innumerable examples of the law of divergence of form, which is called also the law of adaptive radiation Almost every successful class or order of vertebrate animals, for example, has members that have adjusted themselves to all of the main modes of living Thus among lizards, for example, there are primitive

running forms that prefer the surface life and swift motion, subterranean burrowing types that sometimes are limbless like snakes, and are blind, many arboreal or climbing types, a few volant or flying types, a few ant eating types, and several more or less completely aquatic types Each of these types has the customary adaptations for its own mode of life

We see then, that whether divergent structures are molded into a semblance of similarity to fit a definite environment, or whether similar structures are modified in diverse ways to fit various divergent environments, the adaptation is related very definitely to the environment and to the functional life of the organism No wonder, then, that so many biologists consider that the environment has been a molding force in the evolution of adaptations

General considerations—Adaptations are characteristic of all living organisms and must be accounted for by any evolutionary theory that is to be acceptable Any theory that claims to account for new species but does not account for adaptations is at best only a partial explanation All of the phenomena which have been briefly mentioned in this chapter together with the more intricate phases of general adaptiveness involved in the idea of " the web of life " are part of the background of Darwinism and were in the mind of Darwin when he thought out the great generalization called ' natural selection The 'web of life idea has been admirably presented by Professor Thomson Scotland s most skilful and prolific biological writer The present writer feels that no student of evolution should miss the opportunity of getting into the spirit of Darwinism with this distinguished author, and to make this desideratum easily attainable, the chapter is quoted unchanged as part of the general text and immediately follows this discussion

CHAPTER XXIX

THE WEB OF LIFE[1]

J ARTHUR THOMSON

Naturalists in the true sense who study the life of living creatures in nature have always been distinguished by a keen perception of the interrelations of things Whether we take Gilbert White as representing the old school or W H Hudson as representing the new we get from their observations the same impression of nature as a vibrating system most surely and subtly interconnected But it seems just to say that no naturalist before or since, has come near Darwin in his realisation of the web of life in his clear vision and picture of the vast system of linkages that penetrates throughout the animated world

Correlation of organisms as well as correlation of organs —In thinking of a living body we are accustomed to the idea of the correlation of organs It is of the very nature of an organism that there should be mutual dependence among its parts The organs are all partners in the business of life and if one member changes others also are affected This is especially true of certain organs that have developed and evolved together, and are knit by close physiological bonds We know in health how nerve and muscle, brain and sense organs heart and lungs are closely bound together in the bundle of life We know in disease that a change in one organ often affects another and the fact remains though the nexus is sometimes mysterious The state of our liver may give colour to our whole intellectual firmament and a slight ocular derangement may warp a wise man's philosophy The far reaching importance of a little organ like the thyroid gland beside the larynx is well known, our intellectual as well as our bodily health depends on its soundness Now, just as there is a correlation of organs within the body so there is a correlation of organisms in that system of things which we call Nature In both cases we are here using the word ' correlation" in its deeper sense—

[1] From J A Thomson *Darwinism and Human Life* (copyright 1900) Used by special permission of the publishers Henry Holt & Company

that the various parts are more than mutually dependent, that they are in some measure co-ordinated making larger systems workable

What the metaphor of "the web of life" suggests —We may use the metaphor "web of life" in two ways On the one hand, Nature has a woven pattern which science seeks to read, each science following the threads of a particular colour There is a warp and woof in this web, which to the zoologist usually appear as ' hunger ' and ' love " There is a changing pattern in the web, becoming more complex as the ages pass, and *this is evolution* But the essential idea of a web is that of interlinking and ramifying We can never tell where a thread will lead to If one be pulled out, many are loosened This is true of Nature through and through

The phrase "web of life ' suggests another picture—the web of a spider—often an intricate system with part delicately bound to part so that the whole system is made one ' The quivering fly entangled in a corner betrays itself throughout the web, often it is felt rather than seen by the lurking spinner So in the substantial fabric of the world part is bound to part In wind and weather, or in the business of our life, we are daily made aware of results whose first conditions are very remote, and chains of influence, not difficult to demonstrate, link man to beast, and flower to insect The more we know of our surroundings the more we realise that nature is a vast system of linkages, that isolation is impossible "

Dependence of living creatures on their surroundings —We do not know what life in principle is but we may describe living as action and reaction between organisms and their environment This is the fundamental relation—the dependence of living creatures on appropriate surroundings, and the primary illustrations of linkages must be found here The living creatures are real, just in the same sense as the surroundings are real, but it is plain that we cannot abstract the living creatures from their surroundings When we try to do this they die—even in our thought of them, and our biology is only necrology Huxley compared a living creature to a whirlpool in a river, it is always changing, yet always apparently the same, matter and energy stream in and stream out, the whirlpool has an individuality and a certain unity, yet it is wholly dependent upon the surrounding currents One may push the whirlpool metaphor too far, so as to give a false simplicity to the facts, for when vital whirlpools began to be there also emerged what cannot be discerned in crystal or dewdrop—the will to live, a capacity of persistent experience, and the power of giving rise to

other lives To ignore this is to attempt a falsely simple natural history But what Huxley s metaphor of the whirlpool does vividly express is the dependence of living creatures on their surroundings We cannot understand either the whirlpool or the trout apart from the stream

When we think out this fundamental dependence upon surroundings, we see for instance, that all our supplies of energy, all our powers of every kind—with our own hands, or by the use of animals, or by means of machinery—are traceable to the sun Or again, it is easy to show that our society depends fundamentally not on gold, but on iron We depend for food on plants and animals, and through these animals on plants ultimately the plants feed upon air, water, and salts, which, with the aid of the energy of the sunlight, they build up into complex organic compounds, they cannot do this unless the sun shines through a screen of green pigment called chlorophyll, there cannot be chlorophyll without iron, *therefore* our whole social framework is founded on *iron*

Nutritive chains —Plants feed on their inanimate environment in a direct way that is impossible to animals, so we pass insensibly from dependence on surroundings to those *nutritive chains* which bind living creatures together in long series often quaintly suggestive of ' The House That Jack Built ' and similar old rhymes We have ceased to wonder at the circulation of the blood in our body, have we begun to wonder enough at the ceaseless circulation of matter in the system of nature? As Heraclitus said πάντα ῥεῖ, all things are in flux ' The rain falls the springs are fed the streams are filled and flow to the sea the mist rises from the deep and the clouds are formed which break again on the mountain side The plant captures air, water, and salts, and, with the sun s aid, builds them up by vital alchemy into the bread of life, incorporating this into itself The animal eats the plant and a new incarnation begins *All flesh is grass* The animal becomes part of another animal, and the reincarnation continues " The silver cord of the bundle of life is loosed, and earth returns to earth The microbes of decay break down the dead, and there is a return to air and water and salts We may be sure that nothing real is ever lost we are sure that all things flow Penelope-like, Nature is continually unravelling her web and making a fresh start

Nexus between mud and clear thinking —To keep a famous inland fish pond from giving out, some boxes of mud and manure were placed at the sides Bacteria—the minions of all putrefaction—

worked in the mud and manure, making food for minute Infusorians which multiply so rapidly that there may be a million from one in a week's time A cataract of Infusorians overflowed from box to pond, and the water fleas and other small fry gathered at the foot of the fall and multiplied exceedingly Thus the fishes were fed, and, as fish flesh is said to be good for the brain, we can trace a nexus from mud to clear thinking What was in the mud became part of the Infusorian which became part of the Crustacean, which became part of the fish, which became part of the man And it is thus that the world goes round

Correlation between catches of mackerel and amount of spring sunlight—A curious and most interesting correlation has been discovered by Dr E J Allen between catches of mackerel and the amount of sunlight. The more sunshine in May, the more mackerel at Billingsgate How does this work out? Mr G E Bullen shows that "for the years 1903-1907 there appears to be a correlation between the number of mackerel taken during May, and the amount of Copepod plankton, upon which the mackerel feed, taken in the neighborhood of the fishing grounds during the same month" Mr W J Dakin shows that the food of Copepods consists largely of the vegetable organisms of the plankton, such as diatoms, and of Infusoria like organisms called Peridinidae But the production of this microscopic plankton, the "stock" of the 'seasoup," depends partly on the composition of the sea water, partly on the temperature, and partly on the amount of light available There seems to be no correlation between the surface temperature and the abundance of mackerel, but Dr Allen has shown a correspondence between sunshine and the catches Thus we see that, if all flesh is grass, then in the same sense all fish is diatom

Nutritive chains in the deep sea—If we pass from the sunlit open sea to the floor of the deep sea—that strange, dark, cold, silent, plantless world—we find carnivorous animal preying upon carnivorous animal through long series—fish feeds on fish, fish on Crustacean, Crustacean on worm, worm on still smaller fry, and all ultimately depend on the basal food supply—the ceaseless shower of moribund atomies sinking from the surface waters many miles, it may be, over head, like the snowflakes on a quiet winter day

Dependence of one organism on another for the continuance of the species—Passing from "nutritive chains," we may select a few illustrations of the dependence of one creature upon another for the

continuance of its kind The crowning instances are to be found in interrelations between plants and animals which secure cross fertilisation and the distribution of seeds To both of these Darwin devoted much attention, and they were always favourite subjects with him

Everyone knows that flowering plants and flower visiting insects have grown up throughout long ages together, in alternate influence and mutual perfecting They are now fitted to one another as hand to glove The insects visit the flowers for food, in so doing they carry the fertilising golden dust from blossom to blossom, so that the possible seeds become real seeds

In 1793 a Berlin naturalist, Christian Konrad Sprengel, like Darwin in his perception of the web of life, published a pioneer book entitled *The Secret of Nature Discovered in the Structure and Fertilization of Flowers*, in which he showed that most flowers have nectar which insects enjoy, that by the insects' visits pollination is secured, that there is no detail of the flower without its meaning—the colour is a flag to attract the insect's eye, conspicuous spots are honey guides to the explorers, there are arrangements for keeping the pollen dry and for dusting it on the insects, and so on If Sprengel had only discovered the utility of the cross fertilisation, which Darwin proved experimentally, his work could hardly have been overlooked for nearly seventy years In 1841 it came into Darwin's hands, and impressed him as being ' full of truth," although "with some little nonsense ' In Darwin's work Sprengel had his long delayed reward

Darwin's instance of the connection between cats and clover — One of Darwin's instances of the web of life—given in connection with the pollination of flowers—has become familiar all over the world It should never become trite to us and it should never be regarded as more than a particularly clear illustration of a general fact "Plants and animals, remote in the scale of nature, are bound together by a web of complex relations I have found, from experiments, that humble bees are almost indispensable to the fertilisation of the heart s ease (*Viola tricolor*), for other bees do not visit this flower I have also found that the visits of bees are necessary for the fertilisation of some kinds of clover—thus, 100 heads of red clover (*Trifolium pratense*) produced 27,000 seeds, but the same number of protected heads produced not a single seed Humble bees alone visit red clover, as other bees cannot reach the nectar . Hence we may infer as highly probable that, if the whole genus of humble bees became extinct or very rare in England, the heart's-ease and red clover would become

very rare, or wholly disappear" We know that the red clover imported to New Zealand did not bear fertile seeds until humble bees were also imported 'The number of humble-bees in any district depends in a great measure on the number of field mice, which destroy their combs and nests, and Colonel Newman, who has long attended to the habits of humble-bees, believes that more than two-thirds of them are thus destroyed all over England" Now the number of mice is largely dependent, as everyone knows, on the number of cats, and Colonel Newman says 'Near villages and small towns I have found the nests of humble-bees more numerous than elsewhere, which I attribute to the number of cats that destroy the mice" Thus we may say, with Darwin, that next year's crop of purple clover is influenced by the number of humble-bees in the district which varies with the number of field mice, that is to say, with the abundance of cats!

Scattering of seeds —It is a fascinating chapter of natural history which tells us how cross-pollination is effected—here by a bee and there by a butterfly, occasionally by a long billed humming bird beautifully poised before the flower with almost invisibly rapid vibrations of its wings and occasionally by a slowly moving snail of epicure appetite But not less important is the part played by animals in the scattering of seeds, and here again Darwin gives us the classic case of fourscore seeds germinating out of a ball of mud from a bird s foot From one instance you may learn all, and see that much of Darwin's work has been an eloquent commentary on that memorable saying about the sparrow that falls to the ground Such a simple event literally sends a throb through surrounding nature, we can follow its effects a few steps, just as we follow for a few yards the ripples made when we throw a stone into a still lake, in either case can we doubt that the spreading influences are real, though they pass beyond our ken?

Interrelations between fresh-water mussels and fishes —As a striking illustration of the inter linking of different forms of life, we may take the case of the fresh water mussels and their larvae The fertilised eggs develop in the outer gill plate of the mother mussel, and minute bivalve larvae, called *Glochidia*, are formed. The mussel keeps these within the cradle until a fresh water fish—such as the minnow—comes into the vicinity, and then she sets them free In a way that we do not understand, the simple constitution of the larvae is tuned to respond to the presence of minnows and the like, and with snapping valves they manage to fix themselves to their host. After a short

period of temporary parasitism, at the end of which there is a metamorphosis they drop off from the fish into the mud, often far from their birth place This is curious enough but the idea of linkages becomes incandescent in the mind when we note that, just as the fresh water mussel has young temporarily parasitic on fishes, so a fresh water fish the bitterling (*Rhodeus amarus*), has its young temporarily parasitic in the gills of the mussel

Life-histories of parasites—When we pass to parasites in a stricter sense we find the most extraordinary interconnections the most widely separated animals often sharing a parasite between them Liver rot, which has repeatedly killed a million sheep in a year in Britain alone, is due to a parasite which passes from sheep to water, from water to water snail, from water snail to grass, from grass to sheep The tapeworm of the cat has its bladder worm stage in the mouse, the sturdie worm of the sheep s brain has its tape worm stage in the dog, and similar relations hold for hundreds of species The troublesome threadworm of human blood (*Filaria sanguinis hominis*) is transferred from man to man by the mosquito, and the guinea worm which was probably the fiery serpent that vexed the Israelites in the desert, which passes into man in drinking water, spends its youth in a minute water flea, called by the giant s name of Cyclops The importance of tse-tse flies in transmitting the minute animals which cause sleeping sickness and allied diseases is known to all We have spoken of the connection between cats and clover, and there is a not less striking connection between cats and plague For it seems to have been shown in India that the more cats the fewer rats, and the fewer rats the fewer rat fleas, which are the agents in passing the plague-germs to man

Far-reaching influence of certain animals, earthworms—We realise the idea of the web of life in another way when we consider the far reaching influence of particular kinds of activity the best instance being the work of earthworms In 1777 Gilbert White got at the very root of the matter "The most insignificant insects and reptiles are of much more consequence and have more influence in the economy of nature than the incurious are aware of Earthworms, though in appearance a small and despicable link in the chain of nature, yet, if lost, would make a lamentable chasm Worms seem to be the great promoters of vegetation, which would proceed but lamely without them, by boring perforating, and loosening the soil, and rendering it pervious to rains and the fibres of plants, by drawing straws and

stalks of leaves and twigs into it, and, most of all, by throwing up such infinite numbers of lumps of earth called worm casts, which, being their excrement, is a fine manure for grain and grass Worms probably provide new soil for hills and slopes where the rain washes the earth away, and they affect slopes probably to avoid being flooded

The earth without worms would soon become cold, hard bound, and void of fermentation, and consequently sterile These hints we think proper to throw out, in order to set the inquisitive and discerning at work A good monograph of worms would afford much entertainment and information at the same tim- and would open a large and new field in natural history '

The monograph that Gilbert White wished for in 1777 was published by Darwin in 1881, the year before he died—"the completion, ' he said, "of a short paper read before the Geological Society more than forty years ago " With his characteristic thoroughness and patience he worked out the part that earthworms have played in the history of the earth, and proved that they deserve to be called the most useful animals By their burrowing they loosen the earth, making way for the plant rootlets and the raindrops, by bruising the soil in their gizzards, they reduce the particles to more useful, powdery form, by burying the surface with castings brought up from beneath they have been for untold ages ploughers before the plough and by burying leaves they have made a great part of the vegetable mould over the whole earth. In illustration of the last point, we may notice that we recently found thirteen midribs of the leaves of the rowan, or mountain ash, radiating round one hole like the spokes of a wheel, the withering leaflets had been carried down, and two were sticking up at the mouth of the burrow, that meant 91 leaflets to one hole Darwin showed that there often are 50,000 (and there may be 500 000) earthworms in an acre, that they often pass ten tons of soil per acre per annum through their bodies, and that they often cover the surface at the rate of three inches in fifteen years Though our British worms only pass out about 20 oz of earth in a year, the weights thrown up in a year on two separate square yards which Darwin watched were respectively 6 75 lb and 8 387 lb , which correspond to 14½ and 18 tons per acre per annum

We follow the work further and it becomes evident that the constant exposure of the soil bacteria on the surface is bound to be important, on the one hand, in allowing them to be scattered by wind and rain, on the other in exposing them to the beneficent action of the

sunlight—which is the most universal, effective, and economical of all germicides

In Yorubaland, on the West Coast of Africa, Mr Alvan Millson calculated that about 62,233 tons of subsoil are brought every year to the surface of each square mile, and that every particle of earth, to the depth of two feet, is brought to the surface once in twenty seven years It need hardly be added that the district is fertile and healthy

Earthworms play their part in the disintegration of rocks, letting the solvent humus-acids of the soil down to the buried surface Their castings on the hill slopes are carried down by wind and rain and go to swell the alluvium of the distant valleys or the wasted treasures of the sea The well known parallel ledges along the slopes of grass clad hills are partly due to earthworm castings caught on sheep tracks, and thus we begin to connect the earthworms not only with our wheat supply but with our scenery Well may we say, with Darwin "It may be doubted whether there are many other animals which have played so important a part in the history of the world as have these lowly organised creatures" Those who wish to understand Darwinism should always begin with Darwin's last book—*The Formation of Vegetable Mould through the Action of Worms* (1881) It illustrates the web of life, the idea of which is essential to an understanding of the struggle for existence and natural selection But it also illustrates what Darwin had learned from Lyell—that great results may be brought about by accumulation of infinitesimal items As Professor A Milnes Marshall said 'The lesson to be derived from Darwin's life and work cannot be better expressed than as the *cumulative importance of infinitely little things*"

Termites, or white ants —Henry Drummond, in his *Tropical Africa*, tried to make out a case for the agricultural importance of termites, or white ants It is well known that these old fashioned insects have a pruning action in the forest, destroying dead wood with great rapidity Houses and furniture, fences and boxes, as well as forest trees, fall under their jaws In some places, "if a man lay down to sleep with a wooden leg, it would be a heap of sawdust in the morning" But what of the termites agricultural importance? The point is that they keep the soil circulating by constructing earthen tunnels up the sides of trees and posts and by making huge obelisk like ant hills, or termitaries "The earth tubes crumble to dust, which is scattered by the wind, the rains lash the forests and soils with fury, and wash off the loosened grains to swell the alluvium of a distant

valley" It must be noted, however, that Drummond did not prove his case with sufficient precision, and there is, as Escherich points out in his beautiful study of termites, this difficulty, that, while the castings of earthworms are soft and loose, the earth tubes and constructions of termites are stony

Escherich does, however, admit that the termites have some agricultural importance, and he points out that there are other services to be put to the credit side of their account. They prune off wood that has begun to go, they destroy rotting things, including the bodies of small animals, they make for cleanliness and health In some low lying tracts, as Silvestri has shown, there are dry stretches, "termite islands," which have been gradually built up from the broken-down remains of termitaries Nor should it be forgotten that the white ants are often used as food On the other hand, Escherich does not hesitate to rank them as among the great hindrances to the spread of civilisation They insidiously devour everything wooden from the telegraph post to the wooden butt of the gun hanging against the wall, from books in the library to corks in the cellar There does not seem sufficiently precise information in regard to the living plants that they attack, and no safe general statement can be made except that their appetite is large and catholic.

With a centre in earthworms what a variety of interests must be included within the radius of their life and work!—centipedes, birds, moles, seedlings, man The same is true of termites, and two further illustrations may be given Observers have reported about thirty different species of termites with the habit of feeding on fungi grown within the termitary on specially constructed mazy beds The habit is interesting in many ways, for instance, because the fungi afford a supply of nitrogenous material which is scarce in the ordinary diet of wood, and also because a similar habit occurs in the quite unrelated true ants Finally, the web is illustrated by the numerous boarders, mostly beetles, that are found in the termitaries—not hostile intruders or parasites, but guests which are fed and cared for apparently for the sake of a palatable exudation with a pleasant, narcotising effect on the termites With a centre in termites, what a variety of interests must we not include within the radius of their life and work!—fungi and trees, beetles and birds lizards and anteaters, and man more than any

The hand of life upon the earth —The hand of life has been working upon the earth for untold ages Take plants, for instance The seaweeds lessen the force of the waves, the lichens eat into the

rocks the mosses form huge sponges on the moors which keep the streams flowing in days of drought Many little plants are forever smoothing away the wrinkles on the earth s—their mother's—face, and they adorn her with jewels Others that have formed coal have enriched her with ages of entrapped sunlight The grass—which began to appear in Tertiary ages—protects the earth like a garment, the forests affect rainfall and temper climate, besides sheltering multitudes of living things to many of whom every blow of the axe is a death knell No plant, from bacterium to oak tree, lives or dies to itself or is without its influence upon the earth So among animals there are destructive borers and burrowers and conservative agents, such as the coral polyps and the chalk forming Foraminifera

Practical importance of a realisation of the web of life —What has Darwinism to do with human life? The answer at this stage in our inquiry is clear we must respect the web of life if we wish to master Nature She must be humoured, not bullied Emerson included in his vision of a perfected earth the absence of spiders, but the absence of spiders—which snare so many injurious insects—would mean the absence of much else man probably included In a northern county in Scotland the proprietors were justly annoyed at the injuries inflicted on young trees by squirrels, and they formed a squirrel club setting a price on the beautiful rodent's head Perhaps a wiser course would have been to begin by inquiring what disturbance of the balance of nature had allowed the squirrels to multiply so disastrously But after a period of squirrel-slaughter and some jubilation thereat a cloud began to rise in the sky The wood pigeons were multiplying worse than ever and the farmers at least, said with no uncertain voice that they preferred the squirrels An imperfect recognition of the web of life had left out of account the notable fact that squirrels destroy large numbers of young wood pigeons

One of the hopeful symptoms of the last few years is the reawakening of an interest in woods and forests Everyone knows how terribly these have been wasted, and how the disastrous results have affected rainfall and irrigation, climate and crops and even the character of the people Here what was once a pleasant stream is now like a gravelly road and there the fertile plains are flooded, here the wind is sweeping away the soil, and there both beauty and health have departed The birds which the woods once sheltered are driven elsewhere, and the insect pests are rife among the crops For "the cheapest and most effective insecticides are birds"

The recognition of consequences—often far reaching—grows with us as we work with the idea of the web of life, as we see in proper perspective the criminality of those who are ruthless President Roosevelt has declared his abomination of "the land skinner"—"the individual whose idea of developing the country is to cut every stick of timber off it, and then leave a barren desert for the home-maker who comes in after him That man is a curse, and not a blessing to the country The prop of the country must be the man who intends so to run his business that it will be profitable to his children after him Every right thinking man, and especially those who have grasped the idea of the web of life, will say with Roosevelt, "I am against the land skinner every time"

It may be said that man must exterminate a good deal if he is to go on peaceably with his business, and it will be admitted that there has never been a strong enthusiasm, humanitarian or otherwise, against the elimination of rattlesnakes, and such like The naturalist's answer is that every crusade should be carefully considered on its own merits, and that every careless and hasty destruction of life is to be condemned Even in regard to snakes killing may be carried too far Some creatures are, as it were, on the fringes of the web, while others occupy a position where many threads meet It is scientifically and aesthetically deplorable that birds like the great auk and mammals like the quagga should have been exterminated, but it is practically much more deplorable that we have lost so many hawks and weasels and other members of that pertinacious army whose guerilla warfare keeps hundreds of more humdrum creatures up to the scratch, and keeps "vermin" from becoming a plague Moreover, it is extremely difficult to tell what may be the consequences of exterminating any creature—remote as it may seem from the beaten track of human affairs. One of the obvious lessons of Darwinism is that we should be slow to call any change unimportant Everything counts, or may count A so-called unimportant animal is destroyed and no immediate ill effects are seen But who can tell?

Very pertinent, for instance, is the question What about the parasites that used to complete their life-history in romantic routine in this extinguished animal? Have we extinguished the parasite also? Or is it waiting, with a whip of scorpions, to chastise mankind for their ignorance of Darwinism?

The practical importance of recognising the web of life has been proved by the heavy penalties which man has often had to pay for

disturbing the balance of nature, careless of results and ruthless of beauty, for not admitting that if we would master Nature we must first understand her How much has Australia had to pay for the introduction of rabbits in 1860, or America for sparrows? Sometimes the introduction has been unconscious, and man has only to blame himself for letting the intruder take hold as in the case of the Phylloxera in France, or of the Colorado Beetle in Ireland "Ignorance of nature," Mr A H S Lucas says, ' is costly By disturbing the balance of nature, man has introduced foes into his own household" Speaking of Australia, he says "How much is needed for the eradication of Bathurst Burr, Prickly Pear, Water hyacinth, Bramble and Sweetbriar, Codlin Moth Waxy Scale, Pear Slug and Red Spider, owing to carelessness or lack of knowledge in early days?"

An obvious moral is that we should be careful in our introductions of new organisms—man included—into new surroundings The primary consequences may be predictable, but the secondary and the tertiary consequences—who is sufficient for these things? We have records of the unconscious introduction of rats into Jamaica, where they became a pest To destroy them mongooses were imported, and the rats were soon checked But the mongooses, having finished the rats, began to eat up the poultry and young birds of various kinds As this went on the injurious insects and ticks, that the birds used to eat, began to gain the ascendant A recent report—which requires confirmation—says that the increase of ticks is making life a burden to the mongooses Thus a balance will be again arrived at There is no doubt of that, but how much is often unnecessarily lost by the way!

CHAPTER XXX

NATURAL SELECTION

In the Appendix will be found a chapter of excerpts from Darwin's *Origin of Species*. In this chapter he offers four objections to his theory and attempts to answer them. These four objections are not by any means all that Darwin foresaw, for he presented in another chapter a discussion of "Miscellaneous Objections to the Theory of Natural Selection." Before entering upon a general criticism of Darwinism it would be advantageous to have before us a brief and pointed summary of Darwin's theory—natural selection—now known technically as "Darwinism." The writer knows of no better short statement of the true content of Darwinism than the following summary by Professor Vernon L. Kellogg.

SUMMARY OF DARWIN'S NATURAL SELECTION THEORY[1]

"Darwinism may be defined as a certain rational, causo-mechanical (hence, non-teleologic) explanation of the origin of new species. The Darwinian explanation rests on certain observed facts, and certain inductions from these facts. The observed facts are (1) the increase by multiplication in geometrical ratio of the individuals in every species, whatever the kind of reproduction which may be peculiar to each species, whether this be simple division, sporulation, budding, parthenogenesis, conjugation and subsequent division or amphimixis (sexual reproduction), (2) the always apparent slight (to greater) variation in form and function existing among all individuals even though of the same generation or brood, and (3) the transmission, with these inevitable slight variations, by the parent to its offspring of a form and physiology essentially like the parental. The inferred (also partly observed) facts are (1) a lack of room and food for all these new individuals produced by geometrical multiplication and consequently a competition (active or passive) among those individuals having any ecologic relations to one another, as, for example, among

[1] From V. L. Kellogg, *Darwinism To-Day* (copyright 1907). Used by permission of the publishers, Henry Holt & Company.

those occupying the same locality, or needing the same food, or needing each other as food, (2) the probable success in this competition of those individuals whose slight differences (variations) are of such a nature as to give them an advantage over their confrères which results in saving their life, at least until they have produced offspring and (3) the fact that these "saved" individuals will, by virtue of the already referred to action of heredity, hand down to the offspring their advantageous condition of structure and physiology (at least, as the "mode" or most abundantly represented condition among the offspring)

'The competition among individuals and kinds (species) of organisms may fairly be called a struggle This is obvious when it is active, as in actual personal battling for a piece of food or in attempts to capture prey or to escape capture, and less obvious when it is passive, as in the endurance of stress of weather, hunger, thirst, and untoward conditions of any kind The struggle is or may be, for each individual threefold in nature (1) an active struggle or competition with other individuals of its own kind for space in the habitat, sufficient share of the food, and opportunity to produce offspring in the way peculiar and common to its species, (2) an active or passive struggle or competition with the individuals of other species, which may need the same space and food as itself, or may need it or its eggs or young for food and (3) an active (or more usually passive) struggle with the physico-chemical external conditions of the world it lives in, as varying temperature and humidity, storms and floods, and natural catastrophes of all sorts For any individual or group of individuals any of these forms of struggle may be temporarily ameliorated, as is (1) the intra specific struggle among the thousands of honey bee individuals living together altruistically, in one hive, or (2) the inter specific struggle, when two species live together symbiotically as the hermit crab *Eupagurus* and the sea anemone *Podocoryne*, or (3) the struggle against untoward natural conditions as in special times or places of highly favourable climate, etc. Or for any individual or group of individuals all forms of the struggle may be coincidently active and severe The resultant of these existing conditions is, according to Darwin and his followers, an inevitable natural selection of individuals and of species Thousands must die where one or ten may live to maturity (i e., to the time of producing young) Which ten of the thousand shall live depends on the slight but sufficient advantage possessed by ten individuals in the complex struggle for

existence due to the fortuitous possession of fortunate congenital differences (variations) The nine hundred and ninety with unfortunate congenital variations are extinguished in the struggle and with them the opportunity for the perpetuation (by transmission to the offspring) of their particular variations There are thus left ten to reproduce their advantageous variations. The offspring of the ten of course will vary in their turn, but will vary around the new and already proved advantageous parental condition among the thousand, say, offspring of the original saved ten the same limitations of space and food will again work to the killing off before maturity of nine hundred and ninety, leaving the ten best equipped to reproduce This repeated and intensive selection leads to a slow but steady and certain modification through the successive generations of the form and functions of the species, a modification always toward adaptation, toward fitness, toward a moulding of the body and its behaviour to safe conformity with external conditions. The exquisite adaptation of the parts and functions of the animal and plant as we see it every day to our infinite admiration and wonder has all come to exist through the purely mechanical, inevitable weeding out and selecting by Nature (by the environmental determining of what may and what may not live) through uncounted generations in unreckonable time This is Darwin's causo-mechanical theory to explain the transformation of species and the infinite variety of adaptive modification A rigorous automatic Natural Selection is the essential idea in Darwinism, at least in Darwinism as it is held by the present day followers of Darwin "

OBJECTIONS TO SELECTION

1 Darwin in a letter to his friend Hooker (January 11, 1844) expresses his contempt of Lamarck's ideas in the following words "Heaven defend me from Lamarck's nonsense of a tendency to progression,' 'adaptations from the slow willing of animals,' etc. Lamarck's work appeared to me to be extremely poor, I got not a fact or idea from it "

In spite of these views Darwin s *Origin of Species* is interlarded with Lamarckian explanations Whenever the author feels the short comings of the selection factor he lapses into an explanation involving the idea that the effects of use and disuse of organs are inherited Followers of Darwin, especially Weismann, felt this to be the chief defect in the fabric of Darwinism and bent their efforts chiefly toward purging Darwinism of all taint of Lamarckism.

2 Darwin insisted upon the idea that minute fluctuating variations, which we now know are to a large extent non heritable, were the principal if not the sole, materials for natural selection to work upon He knew of a considerable number of "sports" or "saltatory variations" (now called mutations), but considered these too infrequent to furnish the necessary basis for selection We now know that mutations may be as small as fluctuating variations or as large as "sports" and that they are of much more frequent occurrence than Darwin supposed

3 Darwin considered all variations as heritable He did not distinguish between *somatic* variations and *germinal* variations. In fact, as we learn from a study of his pangenesis theory, he considered all variations as in the first instance somatic, and subsequently transferred by means of gemmules to the germ cells Every somatic variation whether induced by use, disuse, in response to environmental stimulus, or through mere spontaneous variability, was supposed to be able to give off gemmules into the blood stream that would carry to the germ cells the physical basis of the varying character The pangenesis mechanism is now known to have no basis in fact

4 The natural selection theory is based upon a mistaken conception of the methods of artificial selection Darwin believed without having any proof for this belief, that the way in which domestic varieties had been so profoundly modified at the hands of man was by the conscious or unconscious selection of slight fluctuating variations in favorable or desired directions, and that this resulted in the cumulative improvement or enhancement of the desired characters over a long series of generations Darwin supposes that the radically changed conditions of domestication hasten and stimulate variability, thus offering a better opportunity for selection Transferring this idea to nature, he thinks that changed natural conditions stimulate variability, just as does domestication, and that this is seized upon by natural selection to make for adaptation to the new environment and the resultant origin of new species

Our modern experimental studies have shown that somatic modifications due to environmental changes are not hereditary, and that all of the recent domestic varieties whose origin has been observed have been the result of suddenly appearing germinal variations or mutations, that arrive fully formed and cannot be improved by selection, except that they usually need to be selected out or isolated in

order to prevent swamping out through intercrossing with the parent type

5 Objection has frequently been made to Darwin's idea of the purely fortuitous or chance character of variations According to this view variations occur in all structures and in all directions at haphazard, so that there would be the widest possible opportunity for a given adaptive variation to occur just when the circumstances would demand It now appears that variations do not occur in all directions in random fashion but that they tend to follow certain definite paths of change, in other words, variations are, to a consider able extent at least, orthogenetic If variat ons really tend to follow certain definite lines, owing to purely internal causes, natural selection would be unnecessary, at least until orthogenesis went too far for the good of the species, or far enough to be of real importance in the struggle for existence

6 The difficulty of explaining how natural selection could make use of the initial stages of adaptive structures is obvious It is incon ceivable that the first, almost imperceptible variation in a favorable direction could be of selective value, so as to effect the survival of the individual or the relative number of its offspring What would be the advantage of the first few hairs of a mammal or the first steps toward feathers in a bird when these creatures were beginning to diverge from their reptilian ancestors? This objection is of course based on the fluctuating variation idea If the mutation idea were substituted, the difficulty would, to a great extent clear up, for a mutation might be of sufficient importance in one generation to have selective value from the very first

7 Natural selection is said to be incapable of explaining the origin of coadaptive and highly complex adaptations whose effectiveness depends upon the perfection of their adjustments to one another For example, we may refer to some of the perfected adaptations described in chapter xiv In the case of the electric organs of certain fish, the Darwinian assumption would be that the first step in the direction of an electric organ would be a very small one, and that it was built up little by little by means of natural selection But, say the critics, the electric organ would be of no value until it became powerful enough to impart an effective shock to the intruder, and this would not be possible if the character began in a small way The whole phenome non of protective resemblance is open to the same type of criticism As a specific example of this we may cite the case of the dried leaf

butterfly, *Kallima*, previously described (pp 226–228) In its present condition this animal has a strikingly detailed resemblance to a dried leaf, which is therefore doubtless of some value But of what value would be the first tiny change in the direction of resemblance? Until its resemblance became close enough actually to deceive the enemies of butterflies, the critics claim, there would be no chance for selection to act.

8 It is frequently objected that a vast number of characters of organs are useless or non adaptive and, as such, could not have arisen through the instrumentality of natural selection If these useless characters, which are sometimes quite large and prominent, are independent of natural selection why do we need natural selection to explain adaptive characters? It is also claimed that a vast number of specific peculiarities are useless and therefore could not have helped in the differentiation of species It should be said in defense that Darwin realized this difficulty quite as clearly as do his critics and was greatly puzzled by it His idea of correlated variability, however, helps to answer it, for it may well be that many of these apparently useless characters are correlated, or linked in inheritance, with characters of supreme selective value such as general hardiness or great fecundity Darwin also points out that we are not in a position at present to pronounce judgment on the value of many structures or functions that have been adjudged non adaptive

9 Certain characters in organisms past and present, have been interpreted as overspecializations, organs that have evolved beyond the range of usefulness or that are more elaborate than is demanded for survival under the conditions of life The case of the extinct Irish elk is often cited as an example of overspecialization This group of animals went to extremes in the development of size and elaboration of horns far beyond the range of usefulness, so that it is said to have brought about the extinction of the race Natural selection, which is supposed to have brought the horns up to the point of adaptive perfection, should have kept them within the bounds of usefulness

Again the enormously overgrown and overspecialized dinosaurs of long ago are thought of as having followed their lines of evolution far beyond the point of greatest effectiveness and adaptability

10 The rudimentation of structures, which is such a common phenomenon in nature, is said to meet with no adequate explanation on a selection basis The case of the whale's vestigial hind limbs is a case in point Darwin's explanation would be that under aquatic conditions the first whale ancestors would be handicapped by hind

legs and that any decrease in their size, which would be enhanced by disuse, would be of advantage. This might seem reasonable during the main period of limb reduction but, after the limb is reduced to a subcutaneous rudiment, there could be little advantage in carrying the rudimentation still farther Some whales have the hind limbs much more profoundly reduced than others although they are all thoroughly out of the way and involve no hindrance in swimming Any number of similar cases of the same kind might be cited Darwin had no explanation to offer except a resort to Lamarckism, but Weismann the ablest neo-Darwinian, offered the theory of panmixia to cover this objection, a theory which is mentioned in chapter i and will be discussed later

11 It is objected that unless favorable variations occur in a large *number of individuals at the same time the character would be* swamped out by intercrossing with individuals not possessing the favorable variation The probability that such a swamping-out would occur was shown mathematically by various critics By way of answer to this objection there arose a number of ' isolation theories ' according to which favorably varying individuals would be protected from back-crossing with the non varying individuals We might also point out that the Mendelian laws of dominance and segregation would serve to prevent loss of any new favorable character

' 12 It is objected that natural selection might explain the ' sur vival but not the arrival, of the fittest ' But Darwin met this perfectly when he said ' Some have even imagined that natural selection induces variability, whereas it implies only the preservation of such variations as arise and are beneficial to the being under its conditions of life."

13 Criticism has been directed against natural selection because of the fact that some of the supporters of Darwinism notably Weismann have made the claim that natural selection is the sole cause of evolution This idea of the *Allmacht* or all-sufficiency of natural selection was not Darwin's as is clear from the following statement

I am convinced that natural selection has been the most important, but not the exclusive means of modification '

14 It is objected that many if not most of the fluctuating varia tions with which Darwinism deals are purely quantitative or plus-and minus variations whereas the differences between species are qualitative. This is a serious objection and difficult to meet, yet a fair defense has been formulated by leading neo-Darwinians

15 There is a growing skepticism on the part of biologists as to the extreme fierceness of the struggle for existence and of the consequent rigor of selection It may be answered that no very obvious fierceness is implied in the theory So long as overproduction and a shortage of space and food exists the struggle for existence is inevitable

16 Special objections are offered to the subsidiary theory of sexual selection It is said that the type of sexual selection involving active rivalry and battling for mates needs no special theory, inasmuch as this is a mere phase of the struggle for the maintenance of the full life, including the chance to leave offspring It is against the other side of sexual selection, which involves passivity on the part of the male and active choice on the part of the female of the more beautiful or otherwise attractive male, that objection is raised It is claimed that such choice implies too high aesthetic powers in animals of relatively poor vision and mentality Experiments have been performed with moths, in which the male and female coloration is strikingly different, in order to determine whether females actually do exercise any choice of mates that is based on considerations of appearance The result proved conclusively that color patterns have no value in mating, but that the female is passive and mates with the first male to present himself, while the male finds the female through his exquisitely effective sense of smell

We know now, however, that secondary sexual characters are intimately bound up in a physiological way with the functioning of the sex glands and are therefore doubtless to be interpreted as mere non adaptive correlative variations or else as examples of obliterative coloration.

DEFENSE OF SELECTION

In presenting these sixteen objections, we have in most cases indicated the lines upon which the objections have been met, if they have been met. Not all of these objections are considered serious at the present time, for some are based upon lack of a full knowledge of what Darwin actually wrote, others are largely academic in character and fail to stand up under actual test, still others have been more or less adequately met by subsidiary or supporting theories which have been advanced by various neo-Darwinians

Most of the special objections raised in this chapter have received the attention of various able Darwinians, and the student of evolution would doubtless be interested in the expert and fair minded defense

of Darwinism at the hands of Professor V L Kellogg as it appears in his book *Darwinism To Day*

A much briefer and considerably more general defense is that of J L Tayler, which is as follows

GENERAL DEFENSE OF SELECTION[1]

J L TAYLER

To realise how far the theory of selection is capable of explaining the facts of organic evolution it is necessary to bear in mind the postulates in which the theory is founded

1 It is obvious that natural selection can only act by preserving or eliminating the complete organism Selection must therefore be organismal This Darwin and other selectionists have clearly recognised

2 As the whole organism must survive, if the favourable variation or variations are to be preserved it follows that certain minor unfavourable variations may also be preserved if they happen to exist in an individual which survives on account of its major favourable variations And since no individual is completely adapted to its environment, it follows that there must be always a variable amount of residual unfavourable variability in every organism

3 This residual unfavourable variability may be of considerable utility under changed conditions

4 Complementary specialisation of parts as Spencer has shown is favourable to successful competition and as it is the whole organism that is selected or eliminated it follows that any weakness of one specialised part, since it would disturb the balance of all, would be detrimental The more complex the organism, the more specialised the structures, the more dependent one part will be on the others for its existence, hence a complementary specialising tendency will be favoured by selection and therefore all struggles of one part of an organism with another will be reduced to a minimum.

It is clear that there must be some underlying criterion which determines whether any given organism shall be selected or not, and that criterion must be the net result of its adaptability to its environment. One organism may conceivably survive, by its possession of a large number of small favourable variations, while another may survive in virtue of a single valuable one, but in each case it would be

[1] From J L. Tayler "The Scope of Natural Selection" *Natural Science* 1899

the whole value of that organism which determined its survival. This fact is continually disregarded by opponents of the neo Darwinian position, yet this selection of the organism as a whole is the fundamental postulate from which the theory of selection starts Thus it is not uncommom to read criticisms bearing on the early development of some organ, in which the inadequacy of selection is supposed to be proved by the writer demonstrating or believing he has demonstrated, the fact that the particular variation in question must have been too small to be by itself of selection value In many cases the particular variation would, no doubt, if taken alone be, as the objector asserts too unimportant to be selected, but as it is the whole organism that is selected, it is not logical to make an artificial separation and study the development of one organ or structure irrespective of the other organs with which it is in nature associated *Every organ in its evolution must be considered in relation to the whole of the particular organism in which that particular stage of development of that organ is found*

Starting therefore with this fact that the net value of adaptability of the whole organism to its environment must be the basis which determines selection or elimination, it will follow that certain lines of development will result from the application of this criterion In a series of organisms placed under new conditions, elimination will proceed along lines essential to bring about a proper adjustment to the new conditions If the offspring of these adjusted organisms merely repeated in their generation the characters of the exterminated as well as of the surviving organisms, that temporary adjustment would be permanent as long as the conditions were unchanged But since the offspring are produced only by the surviving organisms, selection is continually raised to higher and higher planes of adaptation, and, therefore, as long as conditions remain constant, the tendency of selection must be, as Darwin clearly saw, cumulative He did not, however, apparently see that from this cumulative tendency definite variability must arise out of indefinite

Selection in direct relation to climatic conditions is, therefore, of very minor importance, while selection among the members of a species and all forms of inter-organismal selection is of infinitely more importance, since it is this interaction, produced by the offspring in different degrees inheriting the advantages of both parents (both of whom have survived on account of certain advantages) that leads to the cumulative development and never ending struggle for survival

Darwin came very near to this conception of definite variability when he pointed out that ' if a country were changing, the altered conditions would tend to cause variation not but what I believe most beings vary at all times enough for selection to act on " Extermination would expose the remainder to the mutual action of a different set of inhabitants which I believe to be more important to the life of each being than mere climate, and as ' the same spot will support more life if occupied by very diverse forms it is evident that selection will favour very great diversity of structure

Bearing in mind this cumulative action of selection it will follow that under constant or relatively constant conditions the struggle for successful living will become more and more selective in character, even if the actual number of inhabitants remain more or less the same as when the struggle first commenced The selection of variations will thus tend to pass through certain more or less ill-defined, but *nevertheless, real stages In proportion as the struggle becomes* intense either from the number or from the increasing adaptability of the organisms, or both certain major essential adaptations, which were necessary for the climatic and other more or less comparatively simple conditions will be supplemented by minor auxiliary variations which in the earlier stages would not have appeared And still later, as more and more rigorous conditions of life were imposed, the advantage would tend to rest with those organisms which possessed highly co-ordinated adaptations since this would entail more rapid responsiveness to environment.

As evolution advances from the unspecialised to the specialised and higher and higher forms of life come into being, with increasing complexity and specialisation of parts entailing an increasingly delicate adjustment of those parts to each other s needs, the relation of each part to the whole organism becomes of more and more importance and it follows that selection must become more and more generalised in its action No single variation could be of service to any of the higher forms of life unless it was in more or less complete harmony with the whole tendency of the individual The adjustment of parts and their mutual interdependence make it essential for adaptation that the relation of parts be preserved, consequently, correlated *minute favourable variations will tend to be more and more selected* as evolution passes from the unspecialised to the specialised forms of life This response of the whole organism should be still more delicate in those forms of life that are continually subjecting themselves to

changed conditions, hence this delicacy of adjustment is far more necessary in the higher forms of animal life than in more stationary plant organisms and in the developing nervous systems of animals we have just the central adjusting system that is required for these conditions *With evolution of type there will thus be an increasingly definite tendency given to organic, especially the animal, forms of life, if the acting principle of evolution has been selectional Selection is therefore able to account for the steadily progressive tendency of life as a whole without calling to its aid any unknown and doubtful perfecting principle*

To summarise Natural selection acting on the whole organism tends to produce more and more definite tendencies in all surviving forms of life, which tendencies are progressive and continuous in character Variable conditions, by partially altering the line of selection, induce a temporary indefiniteness And lastly, the process of selection being itself able to be the indirect, though not the direct, cause of those favourable variations which it subsequently selects from is able to dispense with any subsidiary factors provided it has a certain number of elementary properties of life which afford sufficient material to work with

EXPERIMENTAL SUPPORT OF THE EFFECTIVENESS OF NATURAL SELECTION

Weldon's experiments with the shore-crabs of Plymouth Sound — These experiments seem to show that under changed environmental conditions natural selection acts upon minute fluctuating variations of linear or quantitative type so as to produce an alteration in the species exactly as Darwinism would hold A large breakwater was so placed near the mouth of Plymouth Sound that the rate of flow of the river water was greatly slowed down in certain regions This allowed an increased settling of the fine china clay sediment that is carried by the river, and the changed condition caused the death of numerous crabs of the species *Carcinus maenas* The question arose as to whether the survivors and those that had perished showed any consistent differences on the basis of which selection could be operating Careful measurements of hundreds of individuals showed that the mean breadth of frontum is slightly less in the survivors than in the perished Measurements were repeated in two subsequent years and it was found that there was a progressive narrowing of the frontum As an experimental check upon these conclusions Weldon

placed a number of crabs in a large aquarium, in which china-clay was kept partly in suspension, and found that about half of them died Again the survivors were compared statistically with the perished and the same relation was found to hold that the survivors had a mean frontal breadth distinctly narrower than that of the perished Weldon concludes that his experiments have demonstrated two facts about these crabs the first that their mean frontal breadth is diminishing year by year at a measurable rate which is more rapid in males than in females, the second is that this diminution in frontal breadth occurs in the presence of a material namely, fine mud, which is increasing in amount, and which can be shown experimentally to destroy broad fronted crabs at a greater rate than crabs with narrower frontal margins and I see no escape from the conclusion that we have here a case of Natural Selection acting with great rapidity because of the rapidity with which the conditions of life are changing"

Cesnola's experiments with Mantis —To test the selective value of color markings Cesnola fixed specimens of the brown and green *Mantis religiosa* on plants, some of which were against harmonious others against disharmonious backgrounds The result was that most of those which were inconspicuous because of a harmonious background escaped, while most of the others were eaten up by birds

Poulton's and Sanders' experiments with butterfly pupae Numerous pupae of various colors were placed under conditions favoring protective coloration and others under opposite conditions The conclusion was that protective coloration is a real survival factor, and one that operates so as to give the protectively colored individual a decided advantage in the struggle for existence

Davenport s experiments with chickens —A number of chickens some black some white, and some barred or checkered in color, were allowed to wander free in the fields Hawks killed most of the whites and many of the blacks, but spared, to a large extent the less conspicuous checkered and barred types which are harder to detect against a mixed background

All of these experiments merely tend to show that discriminate survival actually occurs but only the experiment of Weldon has a bearing on the possibility that mere quantitative changes of small dimensions might under certain conditions be of selective value We badly need more experimental evidence of this sort and until this is forthcoming we shall have to admit that there is very little

experimental evidence in favor of the type of natural selection that Darwin stood for

THE PRESENT STATUS OF NATURAL SELECTION

It has come to be rather generally believed that the natural selection that Darwin himself believed in stands almost unscathed as one very important causal factor In fact it is the only explanation ever offered for adaptation that even approaches adequacy As an explanation of the origin of new types or new species it falls far short of adequacy and I think Darwin evidently realized this although he was unfortunate enough to entitle his book *Origin of Species* As an explanation of the origin and perfection of adaptation natural selection has only one rival the far less satisfactory Lamarckian theory of the inheritance of acquired characters There is a strong tendency among geneticists to conclude that the modern germ plasm hypothesis with the aid of mutations and the mechanism of Mendelian inheritance furnishes all the necessary explanation of the causes of evolution There is however marked dissent to this extreme position In his critique of De Vries s rather extreme position that the mutation theory needs no aid from natural selection Weismann shows in most able fashion the inadequacy of mutations to account for adaptation and in contrast how well natural selection accounts for them

In a very recent paper Professor C C Nutting attempts to show that natural selection is still an important factor in evolution and quite in harmony with both the mutation theory and Mendelism We perhaps can close the present chapter no more fittingly than by quoting Professor Nutting s paper

THE RELATION OF MENDELISM AND THE MUTATION THEORY TO NATURAL SELECTION[1]

C C NUTTING

Two marked tendencies are evident in the history of any important theory after its publ cation

First The followers of the discoverer carry the theory too far *and attempt too universal an application This is manifestly true* of Wallace and Weismann who out Darwined Darwin in their claims fo natural selection of the followers of Mendel such as Morgan and

[1] From an address given before the Genet cs branch of the American Association for the Ad ancement of Science December 1920 *Science* N S Vol. LIII

Pearl, and of many mutationists who make much greater claims for that theory than does De Vries himself

Second Each generation of biologists is so occupied with its own work and contemporary theories that it makes no real effort to understand preceding theories

This second tendency seems to me most marked in the attitude of present workers along genetic lines towards natural selection. They reveal an apparent lack of understanding of what Darwin really meant and of what he claimed, and when criticising that theory they are often engaged in the classic, but unprofitable, exercise of "fighting windmills"

In view of these facts I hope you will pardon me if I present in as few words as possible just what I believe to be the main factors which Darwin presented as resulting, in their actions and reactions, in natural selection These factors are three in number

First *Heredity*, by which the progeny tend to resemble their parents more than they do other individuals of the same species.

Second *Individual variation*, by which the progeny tend to depart from the parental type and sometimes from the specific type

Third *Geometrical ratio* of increase, by which each species tends to produce more individuals than can survive

Each of these factors is practically axiomatic, so little is it open to argument

No one doubts the fact of heredity, whether pangenesis, Weismannism or Mendelism be the correct expression of the mechanism involved. These do not affect the fact of heredity nor invalidate it as a factor in natural selection

No one doubts the fact of variation, whether it is the "individual variation" of Darwin, the 'fluctuating variety' or the "mutation" of De Vries. All that is necessary for Darwin's purpose is that there be heritable variations That there are such things all parties agree and it matters little what you call them They are adequate to act as a factor in the Darwinian scheme

No one doubts the fact of geometrical ratio of increase It is a proposition easily capable of mathematical demonstration and that is sufficient for Darwin's purpose

These three factors, then, are not debatable as facts, whatever their mechanism or causes

A moment's reflection will show that geometrical ratio of increase is a quantitative factor, giving an abundance of individuals from

which to select, that individual variation is a qualitative factor, giving the differences which make a selection possible and that heredity is a conservative factor, holding fast those characters which better fit the organism to its environment

Now it seems to me that there is no possible outcome of the necessary action and interaction of these three factors that would not be a selection of some sort Darwin thought it comparable in a large way to the selection by which the stock breeder improves his herd, and therefore called it "natural selection," carefully guarding the phrase from misinterpretation from the teleological angle as well as from a too close parallelism between artificial and natural selection And I believe no one has suggested a more acceptable term for the process of selection resulting from the interplay of natural laws

Three outstanding theories have been advanced since the publication of the *Origin* each involving an advance in our knowledge of the mechanism of heredity on the one hand and the origin of variations on the other

Weismann's theory of the continuity and stability of the germ plasm was of immense importance in its discussion of the mechanism of heredity, and his amphimixis gave a plausible explanation of the origin of variations His results were almost universally regarded as confirming and greatly extending the scope of natural selection

Mendel s theory regarding the purity of the gametes, their segregation in the sex cells and the whole complex Mendelian mechanism so admirably described by Morgan, all of these, fascinating and important as they are, deal with the mechanism rather than the fact of heredity In my opinion their acceptance or rejection does not affect the status of natural selection as a theory of organic evolution

But it is the theory of mutation that has furnished most of the ammunition for the opponents of natural selection, and this in spite of the fact that De Vries, the originator of the mutation theory, expresses himself with great clarity as follows

"My work claims to be in full accord with the principles laid down by Darwin and to give a thorough and sharp analysis to some of the ideas of variability inheritance, selection, and mutation which were necessarily vague in his time"

In 1904 when these words were published, there did seem to be a sharp distinction between the ideas of Darwin and those of De Vries The former believed that natural selection acted upon many small variations and accumulated them until the differences were sufficient

to constitute new species, while De Vries claimed that new species were formed by the sudden appearance by mutations of forms specifically distinct from the parents That mutants were new species!

It seems evident that Darwin did not regard ' saltatory evolution " as the common method, while De Vries did

Darwin believed that individual, usually small, variations furnished the material on which selection acts, while De Vries thought that mutants, usually large variations, furnished the material Both, however, believed thoroughly that natural selection was a *vera causa* of evolution

But things have changed greatly since 1904 The work of Morgan Castle, Jennings and a host of others has shown that many mutations are so small, from a phenotypic standpoint that they are quantitatively no greater than the individual variations of Darwin, and that they are heritable in the Mendelian way

Castle produced a perfectly graded series of hooded rats which exhibits almost ideally the steps by which a new form might be produced by natural selection He says

"If artificial selection can, in the brief span of a man's lifetime, mould a character steadily in a particular direction why may not natural selection in unlimited time also cause progressive evolution in directions useful to the organism?'

Jennings says

' Sufficiently thorough study shows that minute heritable variations—so minute as to represent practically continuous gradations—occur in many organisms some reproducing from a single parent, others by biparental reproduction It is not established that heritable changes must be sudden large steps, while these may occur minute heritable changes are more frequent Evolution according to the typical Darwinian scheme, through the occurrence of many small variations and their guidance by natural selection, is perfectly consistent with what experimental and paleontological studies show us to me it appears more consistent with the data than does any other theory "

Many believers in mutation have been needlessly befuddled by the diverse meanings of "variations" as used by Darwin and De Vries Darwin included in his ' individual variations' both the "fluctuating varieties' and the "mutations" of De Vries Phenotypically they cannot even now be distinguished De Vries himself candidly admits that this was Darwin's attitude, thus proving himself

more clear sighted than many of his followers. All that Darwin needed for his purpose was proof of variations that are heritable, and these are found in mutations be they large or small

Just as Mendelism has to do with the mechanism and not the fact of heredity, so the mutation theory deals with the nature and not the fact of variations Neither, in my opinion, has any implication that is antagonistic to the theory of natural selection

The statement has been made that natural selection ' originates nothing ' because it does not explain the origin of variations I must confess scant patience with this point of view As well say that the sculptor does not make the statue because he does not manufacture the marble or his chisel, or that the worker in mosaic originates nothing because he does not make the bits of stone which he assembles in his design!

The material corresponding to the bits of stone in the mosaic is furnished by heredity and variation, and its quantity by geometrical ratio of increase Natural selection acts in selecting and putting together this material in the formation of new species Thus, in a true sense it seems evident that something new has appeared—something that is, but was not

Another favorite figure, introduced I believe by De Vries, is Natural selection acts only as a sieve determining which forms shall be retained and which shall be discarded This also seems to me to fall short of a complete statement of the truth If the material subjected to the sifting process be regarded as changing with each generation by the addition of variations or mutations if you prefer, some of which are favorable to a nicer adjustment of the species to its environment the figure would be more nearly correct. To make it complete however, the mesh of the sieve must change from generation to generation so that a quantitative variation which would be preserved in one generation would be discarded in a later one But in this case natural selection would do more than a sieve could do It would combine a number of favorable variations in the production of something new, a new species!

In conclusion it seems to me that we are justified in maintaining that Mendelism and the mutation theory, while forming the basis of the most brilliant and important advances in biological knowledge of the last half century, have neither weakened nor supplanted the Darwinian conception of the "Origin of species by means of Natural Selection.'

CHAPTER XXXI

ARE ACQUIRED CHARACTERS (MODIFICATIONS) HEREDITARY?

INTRODUCTORY NOTE —In a previous chapter (chap xvi) under the heading Heredity in Pure Lines it was pointed out that germinal variations are hereditary and somatic variations (modifications) are not hereditary That germinal variations are hereditary and may be produced in a number of different ways was also made clear in the discussion of mutations but the statement that somatic modifications are never in the least hereditary is equivalent to a total denial of the doctrine of the inheritance of acquired characters the so-called Lamarckian theory which was briefly presented in chapter ii

[illegible]

leading students of the problem

MISUNDERSTANDINGS AS TO THE QUESTION AT ISSUE[1]

J ARTHUR THOMSON

The precise question is this *Can a structural change in the body induced by some change in use or disuse, or by a change in surrounding influence, affect the germ-cells in such a specific or representative way that the offspring will through its inheritance exhibit even in a slight degree, the modification which the parent acquired?*

Before we pass to discuss the evidence pro and con it will be useful to notice some frequently recurring *misunderstandings*, the persistence of which would make further argument futile

Misunderstanding I —*How can there be progressive evolution if acquired characters are not transmitted?*—Those who have not thought clearly on the subject often shake their heads sagely and remark that they ' do not see how evolution could have been possible at all unless what is acquired by one generation is handed on to the next " To this we have simply to answer (1) that our first business is to find out the facts of the case, careless whether it makes our interpretation of the history of life more or less difficult, and (2) that in the supply of germinal *variations* whose transmissibility is unquestioned, there is ample raw material for evolution We know a little about the abundant

[1] From J A Thomson *Heredity* (copyright 1907) Used by special permission of the publisher John Murray, London

crop of variations at present supplied, there is no reason to believe that it was less abundant in the past

Misunderstanding II —*Interpretations are not facts* —There are many adaptive characters in plants and animals which may be superficially interpreted as due to the direct result of use and disuse or of environmental influence The Lamarckians have so interpreted them, and the Lamarckian way of looking at adaptations has become habitual to many uncritical minds They see on modern flowers the footprints of insects which have visited them for untold ages, they speak of the dwindling of the whale s hind limbs through disuse, of the hardening of the ancestral horses' hoofs as they left the marshes and ran on harder ground, they picture the giraffe by persistent effort lengthening out its neck a few millimetres every century, as the acacia raised its leaves higher and higher off the ground, and they say that animate nature is so full of evidences of the inheritance of acquired characters that no further argument is needed

But all this is a begging of the question It is easy to find structural features which *may be interpreted* as entailed acquired characters if acquired characters can be entailed Obviously, however, we must deal with what we can prove to be modifications or with what we can plausibly regard as modifications because we find their analogues in actual process of being effected to-day

It is easy to say that the blackness of the negro s skin was produced by the tropical sun, and that it is now part of his natural inheritance It is easy to say this, but absolutely futile Let us first catch our modifications

The Golden Rod (*Solidago virgaurea*) growing on the Alps is precocious in its flowering when compared with representatives of the same species growing in the lowlands Hoffmann found that Alpine forms transplanted to Giessen remained precocious, therefore the acquired precocity had become heritable But there is no evidence that the precocity was acquired, it may have been the outcome of the selection of germinal variations

The African Wart hog (*Phacochoerus*) has the peculiar habit of kneeling down on its fore-limbs as it routs with its huge tusks in the ground and pushes itself forward with its hind limbs It has strong horny callosities protecting the surfaces on which it kneels, and these are seen even in the embryos. This seems to some naturalists to be a satisfactory proof of the inheritance of an acquired character It is to others simply an instance of an adaptive peculiarity of germinal origin wrought out by natural selection

Misunderstanding III.—*Begging the question by starting with what is not proved to be a modification* —There is no relevancy in citing cases where an abnormal bodily peculiarity re-appears generation after generation, unless it be shown that the peculiarity is a modification, and not an inborn variation whose transmissibility is admitted by all Short sightedness may recur in a family-series generation after generation, but there is no evidence to prove that the original short sightedness was a modification In all probability, short-sightedness is in its origin a germinal variation, like so many other bodily idiosyncrasies

In regard to some diseases, such as rheumatism, it is often said dogmatically by those who know little about the matter that the original affection in the ancestor was brought about by some definite external influence—such as a cold drive or a damp bed but it seems practically certain that in all such cases we have to do with an inborn predisposition, to the expression of which the cold drive or the damp bed were merely the liberating stimulus, comparable to the pulling of the trigger in a loaded gun The liberating stimulus is, of course, of great importance, both in the case of the gun's discharge and the organism's disease, but it only goes a little way towards a satisfactory interpretation in either case Not that we can explain the origin of rheumatism or shortsightedness or any such thing—there is no explanation in calling them germinal variations that cropped up but we are almost certain that they never are modifications or acquired characters

Herbert Spencer twits those who are sceptical as to the transmission of acquired modifications with assigning the most flimsy reasons for rejecting a conclusion they are averse to, but when Spencer cites the prevalence of short sightedness among the 'notoriously studious' Germans, the inheritance of a musical talent, and the inheritance of a liability to consumption, as evidence of the inheritance of modifications, we are reminded of the pot calling the kettle black

Over and over again in the prolific literature of this discussion the syllogism is advanced, either in regard to gout or something analogous—

Gout is a modification of the body, an acquired character,
Gout is transmissible,
Modifications are sometimes transmissible.

It may be formally a good argument, but there is every reason to deny the major premise. There is no proof that the gouty habit had an exogenous origin—that it was, to begin with, for instance the direct result of high living, though it is generally admitted that

excesses in eating or drinking may give a stimulus to its expression "The conclusion that I have arrived at," says Prof D J Hamilton, ' is that the gouty habit of body has arisen as a variation, and as such is hereditarily transmissible, and that excess of diet and alcohol merely renders the habit of body apparent" It may also be pointed out that gout and rheumatism and the like are rather *processes of metabolism* than structural modifications though the latter may ensue

After pointing out the irrelevancy of citing cases of the hereditary recurrence of polydactylism haemophilia, colour blindness in man or the absence of horns in cattle or of tails in cats, as instances of the transmission of acquired characters, Prof Ernst Ziegler says ' Only that can be regarded as acquired' which is produced in the course of the individual life, during and after the period of development, exclusively under the influence of external conditions, the term is in no wise applicable to peculiarities which, as one says, arise of themselves from a predisposition already present in the germ"

Misunderstanding IV —*Mistaking the reappearance of a modification for transmission of a modification* —It is of little service to cite cases where a particular modification reappears generation after generation unless it be shown that the change recurs *as part of the inheritance*, and not simply because the external conditions which evoked it in the first generation still persisted to evoke it in those that followed Reappearance is not synonymous with inheritance

Misunderstanding V —*Mistaking re-infection for transmission* — A particular form of the fourth misunderstanding has to do with facts so special that it may be conveniently treated of separately It has to do with microbic diseases It is admitted that a parent infected with tubercle bacillus or with the microbe of syphilis may have offspring also infected But such cases are irrelevant in the discussion Infection, whether before or after birth, has nothing to do with inheritance As Dr Ogilvie says "Wherever the transmission of infectious disease from parent to offspring has been adduced to support the doctrine of the inheritance of acquired characters, it has been done in utter misconception of its meaning and scope"

Medical men have sometimes condescended to make a subtle distinction between "hereditary" and ' congenital" syphilis—the latter manifested at birth, the former some time afterwards! It seems strange that they have failed to recognise that there is no reason to use the word "hereditary" at all in this connection What occurs is an *infection*, and it is theoretically immaterial at what stage the infection occurs A microbe cannot be part of an inheritance

Misunderstanding VI —*Transmission in unicellulars is not to the point* —It is not to the point to cite cases where unicellular organisms such as bacteria or monads have been profoundly and heritably modified by artificial culture so that, for instance the descendants of a virulent microbe have been made to lose their evil potency It is irrelevant because in regard to unicellular organisms we cannot draw the distinction between body and germinal matter apart from which the concept of modifications is of no value In artificial culture the whole character of the unicellular organism—its particular metabolism —is altered it multiplies by dividing into two or more parts which naturally retain the altered constitution But this is worlds away from the supposed case of an alteration in the structure of the little toe so affecting the germ cells that the offspring inherit a corresponding deformation.

Professor L Errera (1899) reported an experiment with a simple but multicellular mould (*Aspergillus niger*) which adapted itself to a medium more concentrated than the normal The second generation of the mould was more adapted than the first, and the adaptation to the concentrated medium was not wholly lost after rearing in the normal medium again This looks like evidence of the inheritance of the acquired adaptive quality which was brought about as a direct modification But the case does not really help us since the distinction between *soma* and *germ plasm* is not more than incipient in the mould in question And even if the distinction were more marked it would only show that the germ plasm is capable of being affected *along with* the body, by a deeply saturating influence which nobody has ever denied

Misunderstanding VII —*Changes in the germ-cells along with changes in the body are not relevant* —Another misunderstanding is due to a failure to appreciate the distinction between a change of the reproductive cells along with the body, and a change in the reproductive cells conditioned by and representative of a particular change in bodily structure The supporters of the hypothesis that modifications may be transmitted point to the tragic cases where some poisoning of the parent s system by alcohol opium, or some toxin is followed by some deterioration in the offspring There is no doubt as to the fact, the question is as to the correct interpretation

1 In some cases it may be that the whole system of the parent is poisoned—reproductive cells as well as body, the effect may be as direct on the germ-cells as on the nerve-cells These, therefore, are not cases on which to test the transmissibility of an acquired character—i.e

of a particular somatic modification If a local poisoning had a structural effect on some particular organ and if that structural effect was reproduced in any degree in the offspring, the case would be relevant, but when the whole organism is soaked in a poison the case is irrelevant If it could be said that the sunshine which brings about sun burning in the skin soaks through the organism even to its reproductive cells and specifically affects them in a manner analogous to the saturating poison we should have a physiological basis for expecting the inheritance of sun burning But we cannot make this assumption We have no warrant for believing that the modification of a part re-echoes in a definite specific way through the organism until even the penetralia of the germ cells reverberate

2 A parent organism is poisoned and there are structural results of that poisoning The offspring are born poisoned, and show similar structural peculiarities This may be due to the fact that the germ cells were poisoned along with the parental body, but it may also be due, in the case of a mother to a poisoning of the embryo before birth in a manner comparable to a pre natal infection

3 In some cases—*e g* of alcoholism in successive generations—there may be poisoning of the germ cells along with the body, there may be poisoning of the embryo before birth, and of the infant after but it may also be that what is really inherited is a specific degeneracy of nature an innate deficiency of control perhaps, which led the parent to alcoholism, and which may find the same or some other expression in the child

Cases are known in which the children of a dipsomaniac father and a quite normal mother have exhibited a tendency to alcoholism insanity, and the like In this case the possibility of poisoning the unborn child is eliminated, but there remain three possibilities of interpretation—that there was specific poisoning of the paternal germ cells that what was inherited was the constitutional weakness which expressed itself as alcoholism in the father, and that there were detrimental influences in the early nutrition, environment, education—"nurture," in short—of the offspring

But while we have admitted a good deal, we have not admitted the transmissibility of a particular structural modification brought about in the parental body as a result of the toxin

Misunderstanding VIII —*Failure to distinguish between the possible inheritance of a particular modification and the possible inheritance of indirect results of that modification, or of changes correlated with*

it.—At first sight this seems hair splitting, but it is a crucial point. Through his vigorous exercise the blacksmith develops a muscular arm worthy of admiration, the shoemaker acquires skeletal and muscular peculiarities less admirable. There are many permanent and profound modifications associated with particular occupations. Are we to believe, it is asked, that the occupation of the parents has no influence on the offspring? Are we to believe, it is asked, that the children of soldier, sailor, tinker, tailor, are in no way affected by the parental functions?

It would be interesting to have precise data in regard to this, but it is generally admitted that when parents have healthful occupations their offspring are likely to be more vigorous. The matter is complicated by the difficulty of estimating how much is due to good nurture before and after birth. It is not unlikely, too, that some profound parental modifications may influence the general constitution, may even affect the germ-cells, and may thus have results in the offspring. But unless the offspring show peculiarities *in the same direction* as the original modifications, we have no data bearing precisely on the question at issue.

A belief in the inheritance of modifications was perhaps expressed in the old proverb, "The fathers have eaten sour grapes, and the children's teeth are set on edge"—a proverb which Ezekiel with such solemnity said was not any more to be used in Israel. Now if "setting on edge" was a structural modification, and if the children's teeth were "set on edge" as their fathers' had been before them, there would be a presumption in favour of the transmission of this acquired character, though it would be still necessary to inquire carefully whether the children had not been in the vineyard too. But if, as Romanes said, the children were born with wry necks, we should have to deal with the inheritance of an indirect result of the parent's vagaries of appetite, and not with any direct representation in inheritance of the particular modification produced in the paternal dentition.

Misunderstanding IX.—*Appealing to data from not more than two generations*.—It has often been pointed out that animals transported to a new country or environment may exhibit some modification apparently the result of the novel influence, and that their offspring in the same environment may exhibit the same modification *in a greater degree*. Thus sheep may show a change in the character and length of their fleece, and their progeny may show the same change more markedly.

But it is perfectly clear that if the evidence does not go beyond this, nothing is proved that affects the question at issue It was to be expected that the offspring should show the modification in a more marked degree than their parents did, since the offspring were subjected to the modifying influences from birth, whereas their parents were influenced only from the date of their importation

What would be welcome is evidence that the *third* generation is more markedly modified than the second, then there would be data worth considering Only then would it be necessary to consider Weismann's somewhat subtle discussion as to the influence of climate

THE INHERITANCE OR NON INHERITANCE OF ACQUIRED CHARACTERS[1]

EDWIN GRANT CONKLIN

Few questions in biology have been discussed so fully and so fruitlessly as this It is a problem of the greatest interest not only to students of biology but also to sociologists, educators and philanthropists and yet it is still to a certain extent an unsolved problem

Opinions of Lamarck and Darwin —It is well known that Lamarck taught that characters due to desire or need, use or disuse, and to changed environment or conditions of life were inherited and thus brought about progressive evolution Long ago desire or need was repudiated as a factor of evolution Lowell satirized it in his *Biglow Papers* in these words

"Some filosifers think that a fakkilty's granted
The minnit it's felt to be thoroughly wanted

That the fears of a monkey whose holt chanced to fail
Drawed the vertibry out to a prehensile tail"

Darwin wrote to Hooker, "Heaven forfend me from Lamarck's nonsense of adaptation from the slow willing of animals , but although he repudiated this feature of Lamarckism he held that characters due to use or disuse and to changed conditions of life might be *inherited* and he proposed his hypothesis of pangenesis in order to explain the process of the transmission of such characters to the germ cells

Weismann's theories —Weismann introduced a new era in biology by denying the inheritance of all kinds of acquired characters and by challenging the world to produce evidence that would stand a

[1] From E. G. Conklin *Heredity and Environment* (copyright 1919) Used by special permission of the publishers The Princeton University Press.

rigorous analysis But Weismann's greatest service lay in his constructive theories rather than in destructive criticism he forever disposed of theories of pangenesis and the like by showing that the germ cells are not built up by contributions from the body and that characters are not transmitted from generation to generation, but on the other hand that there is transmitted a germ plasm which is relatively independent of the body and which is relatively very stable in organization This epoch making theory of Weismann's has naturally undergone some changes, as the result of new discoveries It is no longer believed that the germ plasm is really independent of the body, nor that it is absolutely stable, as Weismann at one time held There is no doubt that the germ cells and the germ plasm are physiologically related to other cells and to other plasms and similarly there is no doubt that the germ plasm although very stable can and does change its constitution under some rare conditions But in the main the germ plasm theory is accepted by the great majority of biologists to-day, and recent work in genetics and cytology has brought many confirmations of this theory

Distinctions between hereditary and acquired characters—As long as it was believed that the developed characters of an organism could be transmitted as such to its descendants it was customary to speak of developed characters as hereditary or acquired and to talk of the inheritance or non inheritance of acquired characters This distinction is not a logical one for all developed characters are invariably the result of the responses of the germinal organization to environmental stimuli, and of course no developed character can be purely hereditary or purely environmental But when a given character arises in many individuals of the same genotype under different environmental conditions it is probable that heredity, which is the constant factor in this case is also the determining factor for that character On the other hand if a character develops in response to peculiar stimuli and does not appear in other individuals of the same genotype in which such stimuli are lacking it is said to be an environmental or acquired character In fine, inherited characters are those whose distinctive or differential causes are in the germ cells, while acquired characters are those whose differential causes are environmental

Statement of problem.—Briefly stated the question of the inheritance of acquired characters is this Can the differential cause of a character be shifted from the environment to the germ plasm? Can

peculiarities of the environment which influence the development of somatic characters so affect the germ cells that they will produce these somatic characters in the absence of the peculiar environment? Can the characteristics of a developed organism enter into its germ cells and be born again in the next generation? Considering the fact that germ cells are cells and contain no adult characteristics it seems very improbable that any peculiarity of environment whether of nutrition, use, disuse or injury, which brings about certain peculiarities of developed characters in the adult, could so change the structure of the germ cells as to cause them to produce this same character in subsequent generations in the absence of its extrinsic cause How, for example, could defective nutrition which leads to the production of rickets, affect the germ cells which contain no bones so as to produce rickets in subsequent generations, although well nourished? Or how can over-exertion leading to hypertrophy of the heart, so affect the germ cells that they, in turn would produce hypertrophied hearts in the absence of over-exertion, seeing that germ cells have no hearts? Or how could the loss or injury of eyes or teeth or legs lead to the absence or weakened development of these organs in future generations seeing that inheritance must be through germ cells which possess none of these structures?

Lack of evidence for inheritance of acquired characters—But, apart from these general objections to the doctrine of the inheritance of acquired characters, there are many special difficulties There is no conclusive and satisfactory evidence in favor of such inheritance Almost all the evidence adduced serves to show only that characters are acquired, not that they are inherited

It is a matter of common observation that mutilations are not inherited, wooden legs do not run in families, although wooden heads do The evidence for the inheritance of peculiarities due to use or disuse is wholly inconclusive, for example, did the giraffe get his long neck because he browsed on trees, or does he browse on trees because he has by inheritance a long neck? Did attempts to fly lead to the development of wings in birds, or do birds fly because heredity has

each of these alternatives rather than of the first.

There still remains the question of the inheritance of certain characters due to environment, though here also the most clear-cut

evidence is against this proposit on That unusual conditions of food temperature, moisture, etc, may affect the germ cells so as to produce general and indefinite variations in offspring is probable, but this is a very different thing from the inheritance of acquired characters The germ cells being a part of the parental organism may be modified by such changes in the environment as affect the body as a whole, they may be well nourished or starved, they may be modified by changed conditions of gravity, salinity, pressure, temperature, etc, and these modifications of the germ cells probably lead to certain general modifications of the adult, which may be larger or smaller, stronger or weaker, according as the germ is well or poorly nourished, but it is incredible that the environment which produces rickets, or hypertrophied heart, or loss of sight in one generation should modify the germ cells in such a peculiar and definite way that they should give rise in the next generation to these particular peculiarities, in the absence of the extrinsic cause which first produced them The inheritance of acquired characters is incredible, because the egg is a cell and not an adult organism, and in this case there is no sufficient evidence that the thing which is incredible really does happen

No inherited influence of stock on graft—If specific changes of environment produced specific changes in heredity we should expect to find that where different plants or animals are grafted together each would modify more or less the hereditary constitution of the other But this does not occur Everybody knows that when a branch of a particular kind of fruit tree is grafted upon a tree of a different variety the quality of the fruit borne by that branch is not altered by its close union with the new stock The same is true of all forms of animal grafts Harrison cut in two young tadpoles of two species of frog, *Rana sylvatica* and *Rana palustris*, and spliced the anterior half of one to the posterior half of the other These frogs and their tadpoles differ in color as well as in other respects *R sylvatica* being more deeply pigmented than *R palustris* In the grafted tadpoles each half preserved its own peculiarities even up to the adult condition

A still more striking case of the persistence of heredity in spite of environmental changes is found in experiments in which the ovaries are removed from one variety of animal and transplanted to another variety Guthrie made such transplantation in the case of fowls and concluded that there was some influence of the foster mother upon the transplanted ovary, but Davenport, who repeated his experiments, was unable to confirm his results Finally Castle and Phillips furnished

the most conclusive demonstration that the hereditary characteristics of the transplanted ova are in no wise changed by the foster mother They removed the ovary from a pure black guinea pig and put it in the place of the ovary of a pure white animal After recovering from the operation this white female with the ' black ' ovary was bred to a pure white male Three litters of offspring from these parents were all pure black Although both parents were pure white all the offspring of the F1 generation were black because they came from ' black eggs and black is dominant over white The fact that these ' black eggs developed in the body of a white female did not in the least change their hereditary constitution

Dominants and recessives remain pure —A still more intimate union takes place when the dominant and recessive characters come together in any zygote These characters, or rather the factors which determine them, may be intimately associated in every cell of the organism throughout an entire generation and yet we may get a clean separation of these characters in the next generation, in many cases neither the dominant nor the recessive character has been at all modified by its most intimate association with the other

Climatic effects not inherited —A striking instance of the purely temporary effect of the environment and of the long persistence of hereditary constitution amidst new environmental conditions, which have greatly changed the appearance of the developed organisms, is found in the case of alpine plants Nageli says that such plants, which have preserved the characters of high mountain plants since the ice age, lose these characters perfectly during their first summer in the lowlands

Summary —If acquired characters were really inherited we should expect to find many positive evidences of this instead of a few sporadic and doubtful cases In particular why do we not find in plant or animal grafting that the influence of the stock changes the hereditary potencies of the graft? Why do we not find that transplanted ovaries show the influence of the foster mother as Guthrie supposed—a thing which has been disproved by Castle? Why do dominant and recessive characters remain pure, even after their intimate union in a hybrid, so that pure dominants and pure recessives may be obtained in subsequent generations from this mixture? Why does every child have to learn anew what his parents learned so laboriously before him? Even the strongest defenders of the inheritance of acquired characters are constrained to admit that it occurs only sporadically and exceptionally

Neo-Lamarckism —Many modifications of the Lamarckian hypothesis of the inheritance of acquired characters have been proposed in recent years Foremost among those are the mneme theory of Semon and the "centro epigenesis ' theory of Rignano To Semon as to many other biologists the apparent resemblance between memory and heredity has seemed significant, and this furnishes the basis of his theory Semon holds that every condition of life every functional activity of an organism leaves a permanent record of itself in what he calls an "engramme" If these conditions or activities are long continued their engrammes are heaped up and affect heredity Semon does not ask if ' acquired characters ' are inherited, but rather ' Are the hereditary potencies of the germ cells altered by stimuli acting on the parental body?" This is a very different thing from the inheritance of a particular acquired character, and there is some evidence that such stimuli may in rare instances produce changes in the hereditary constitution of the germ plasm though these evidences are by no means conclusive

Temporary effects of environment, "induction"—On the other hand certain changes may be produced in germ cells or embryos which last for only a generation or two and then disappear It is well known that plants grown in poor soil are smaller and produce smaller seeds than those grown in good soil, and De Vries, Bauer and Harris find that such seeds produce smaller plants having smaller seeds than do seed of normal size This is an after effect of poor nutrition which changes the amount of food material in the seeds and through this the size of the plant which develops from the seed, but it does not change the hereditary constitution Woltereck found that in *Daphnia* there is an after effect of cold lasting for one or two generations, and this he calls "induction," when the effect lasts for one generation, or "pre induction" when it lasts for two or three generations Whitney found that rotifers poisoned with alcohol were weaker in resistance to copper salts and were less fertile than others, and when brought back to normal conditions the first generation was weak but the second was normal On the other hand Stockard finds that the injurious effects of alcohol on guinea pigs persist through two or more generations In man alcohol may have an ' induction' effect on offspring but fortunately it does not seem to alter hereditary constitution Probably of a similar character are Sumner's results, he found that mice raised in the cold have shorter tails than those raised in higher temperatures and this modified character appears in the next generation If this is an after effect or "induction" it should disappear in the following generations

Kammerer found that salamanders with black and yellow spots when reared on yellow soil gradually lose their black color, becoming more yellow, and their young continue to grow more yellow until finally almost all black may disappear The offspring of such salamanders are said to be more yellow than normal, but this work has been called in question and needs confirmation Even if confirmed the result may be an after effect or "induction" which would soon disappear under usual conditions, and there is no evidence that it is really inherited

Such cases are not instances of true inheritance, they do not signify a change in the hereditary constitution but an influence on the germ cells of a nutritive or chemical sort comparable with what takes place when fat stains are fed to animals, the eggs of such animals are stained, and the young which develop from such eggs are also stained, though the germinal constitution remains unchanged The very fact that the changed condition is reversible and that it disappears within a short time is evidence that it is not really inherited

In conclusion (1) Developed characters, whether "acquired" or not, are never transmitted by heredity, and the hereditary constitution of the germ is not changed by changes in such characters (2) Possibly environmental stimuli acting upon germ cells at an early stage in their development may rarely cause changes in hereditary constitution, but changes produced in somatic cells do not cause corresponding changes in the hereditary constitution of the germ cells. (3) Germ cells like somatic cells may undergo modifications which are not hereditary, if starved they may produce stunted individuals and this effect may last for two or three generations, they may be stained with fat stains and the generation to which they give rise be similarly stained, they may be poisoned with alcohol or modified by temperature and such influence be carried over to the next generation without becoming hereditary All such cases are known as "induction" and many instances of the supposed inheritance of acquired characters come under this category (4) Environment may profoundly modify individual development but it does not generally modify heredity

THE OTHER SIDE OF THE QUESTION

It will have been noted that the chief objection to the idea of the possibility of acquired characters being inherited comes to us as a heritage of the rather extreme Weismannian concept of the "germ

plasm" According to this view as brought out in another place (p 201), there is an unbroken continuity from generation to generation of the germ plasm Germ cells are thought of as remaining entirely undifferentiated for any somatic function and as therefore capable of starting at the beginning to develop a new individual The germ cell is supposed to be 'set apart at an early period in a given individual, it takes no part in the formation of the individual s body, but remains a slumbering mass of potentialities which must bide its time to awaken into expression in a subsequent generation"

Physiologists object to this idea that the germ cells are so distinctly different from body cells and that they are so insulated, as it were, from the soma as to be immune to any changes that may affec the latter Two kinds of data are offered in opposition to this concept A few observers, notably Professor C M Child, have described cases in which somatic cells, that already had become differentiated as primitive muscle cells, lost their differentiation and returned to a germinal condition If this kind of thing were general, and it is probably not, germ cells might conceivably be produced from functioning soma cells and might therefore furnish a mechanism for the transmission of the effects of use and disuse It should be emphasized, however, that, among animals at least, there is extremely little evidence in support of the idea that differentiated body cells give rise to germ cells

Among plants, however, a different situation prevails In the *Begonia*, for example, any part of a plant if cut off is capable of producing a whole new plant Even a purely vegetative organ like a leaf if cut off and partially buried in soil, will bud off a new plant which will produce flowers with perfectly typical germ cells We have to admit, in this case, either that leaf tissues contain undifferentiated germ cells or that somatic tissues give rise to germ cells The first alternative is in harmony with the germ plasm hypothesis, the second is the preferred view of the opponents of this hypothesis

Among animals, as for example annelid worms, it is quite common to find the germ cells aggregated in a few segments of the body If a part of the body in which there are no recognizable germ cells be cut off, it will, under proper conditions, regenerate the lost parts and become a complete worm with functional germ cells The same alternative explanations that were offered for the *Begonia* case apply equally well here Numerous other cases of the same sort are well known to all zoölogists To the advocate of the "germ plasm" theory

they offer no difficulties because he can always fall back upon the statement that, among the lower forms at least, there is reserve germ plasm equally distributed over the whole body ready to differentiate into definite germ cells when needed This type of appeal is abhorrent to the physiologist, and with some justification, for it really begs the question by assuming that any cell that is capable of forming germ cells belongs to the more or less sacred lineage of germ plasm

If we confine the application of the germ plasm idea to the higher animals such as vertebrates and insects we would obviate these chief objections, and the present writer would take the view that it is only among the upper ranges of highly specialized animals that the continuity of the germ plasm concept holds solidly

Another chief objection to the germ plasm concept has to do with the supposed insulation or apartness of the term plasm Physiologists have found that there is an extremely intimate correlation in function between practically all parts of a living organism Many of the structures, such as the rudimentary pituitary body, the thyroids the adrenal body, and various other bodies whose function was long unknown, have now been shown to exercise a profound effect on the development of the whole body Since practically all tissues are known to affect at least some other tissues, is it likely, the physiologist asks, that none of the other tissues affect the germinal tissues? The organism is to be viewed it is said, not as a collection of independently functioning parts but as a single coherent unit On this view no tissue can be thought of as beyond the influence of organic changes

The classic argument of the Weismannians was that *we can conceive of no mechanism* by means of which somatic changes can be carried back into the germ cells, and therefore *there is no such mechanism* Now the fallacy of this argument is obvious, even if we could conceive of no suitable mechanism for this purpose, this does not preclude the existence of such a mechanism Moreover, according to Professor Guyer, just such a mechanism actually exists, as will be brought out in the following quotation from one of his recent publications

A POSSIBLE MECHANISM FOR THE TRANSMISSION OF ACQUIRED CHARACTERS[1]

MICHAEL F GUYER

Some selectionists glibly assert that new characters arise as the result of spontaneous changes in the germ What is meant by this?

[1] From M F Guyer, 'Immune Sera and Certain Biological Problems" *American Naturalist* Vol LV (1921)

Just what is a spontaneous change? No one has ever succeeded in telling us And we may suspect, though perhaps it is heresy to do so, that it is a well sounding phrase that is the equivalent of the three words, "I don't know" Unwilling to admit of the modifying influence of external agencies on the germ, such theorists resort to the fiction of a spontaneous change Coleridge somewhere has said, "What's gray with age becomes religion" We have toyed so long with this idea of germinal continuity and the invulnerability of the germ, that it has become for some of us wellnigh sacrosanct Living matter is living matter wherever it may be found, but when it happens to be in the germ-cells, verily, "this corruptible has put on incorruption and this mortal immortality"!

Now, no one to day, qualified by his knowledge of embryology and genetics to the right of an opinion would, I think, deny that the new organism is in the main the expression of what was in the germ line, rather than of what it got directly from the body of its parents, but does this fact necessarily carry with it the implication that the germ is insusceptible to modification from without? Is not the serum of organisms with blood or lymph an excellent medium through which external influences may operate upon it? Is it not more reasonable to postulate the origination of germinal changes through some such mechanism as this than to attribute it to mysterious "spontaneous changes ?

With such thoughts in mind I and my research associate, Dr E A Smith, set about making various tests Without attempting to tell you of our as yet unsuccessful attempts to secure cytolysins which will operate in the developmental stages of such periodically renewed structures as feathers, or to weary you with the history of our various other failures—of which there are an abundance—I wish to speak briefly about certain antenatal effects we secured in rabbits by means of fowl serum sensitized against rabbit crystalline lens, and of the fact that such induced defects may become heritable

The crystalline lens of the rabbit was selected as antigen, and fowls as the source of the antibodies The lenses of newly killed rabbits were pulped thoroughly in a mortar and diluted with normal saline solution About four cubic centimeters of this emulsion was then injected intraperitoneally or intravenously into each of several fowls. *Four or five weekly treatments with such lens-emulsions were given* Then a week or ten days after the last injection the blood serum of one or more of the fowls was used for injection into pregnant rabbits The rabbits had been so bred as to have the young advanced to about

the tenth day of pregnancy, since from the tenth to the thirteenth day seems to be a particularly important period in the development of the lens It is then growing rapidly and becomes surrounded by a rich vascular network that later disappears From four to seven cubic centimeters of the sensitized fowl serum were injected intravenously into the pregnant rabbits at intervals of two or three days for from ten days to two weeks Several rabbits died from the treatment and many young were killed in utero Of sixty one surviving young from mothers thus treated, four had one or both eyes conspicuously defective and five others had eyes which were clearly abnormal It is possible that still others were more or less affected, since we judged only by obvious visible effects We found later in some of the descendants of these individuals that rabbits which passed for normal during their earlier months subsequently manifested traces of defects in their lenses or in other parts of the eye

The commonest abnormality seen in both the original subjects and in their descendants was partial or complete opacity of the lens usually accompanied by reduction in size Other defects were cleft iris, persistent hyaloid artery, bluish or silvery color instead of the characteristic red of the albino eye, microphthalmia and even almost complete disappearance of the eyeball Taking into account the method of embryological development, however—the relation of lens optic cup, and choroid fissure—the defects are probably all attributable to the early injury of the lens In some cases, both among originals and descendants, an eye microphthalmic at birth may undergo further degeneration such as collapse of the ball and what appears to be a resorption as if some solvent were operating upon it The eyes of the mothers apparently remained unaffected This is probably due to the fact that the lens tissue of the adult rabbit is largely avascular and therefore did not come into contact with the injected antibodies

That the changes in the eyes of the fetuses resulted from the action of lens antibodies is indicated by the fact that in not one of the forty eight controls obtained from mothers which had been treated with unsensitized fowl serum or with fowl serum sensitized to rabbit tissue other than lens, was there evidence of eye defects, and I may add that among the hundred or more young obtained later from mothers which were being experimented upon with various types of sera or protein extracts, for other purposes, not a single case of eye-defect has appeared

As already stated, once the anomaly is secured it may be transmitted to subsequent generations through breeding So far we have succeeded in passing it to the eighth generation without any other than the original treatment. The imperfection, indeed, tends to become worse in succeeding generations and also to occur in a proportionately greater number of young Though not analyzed completely as to its exact mode of inheritance, it has in general, the characteristics of a Mendelian recessive Like such anomalies as brachydactyly or polydactyly in man, the transmission is not infrequently of an irregular unilateral type, sometimes only the right, at others only the left eye showing the defect In the later generations, probably in some measure as the result of selective breeding, there is an increasing number of young which have both eyes affected

To determine whether the reappearance of the defect was due merely to the passing on of antibodies or kindred substances from the blood stream of the mother, or to true inheritance, we mated defective-eyed males to normal females from strains of rabbits unrelated to our defective eyed stock The first generations produced in this way were invariably normal eyed, but when females of this generation were mated to defective eyed males again, we secured defective-eyed young after the manner of an extracted Mendelian recessive It is obvious that in such cases the abnormality could only have been conveyed through the germ cells of the male, and that it is therefore an example of true inheritance Subsequent matings have shown that these young transmit the eye anomalies as effectively as do individuals of the original lines A new strain of defective-eyed young established about the time our original paper went to press, is also flourishing and, as regards transmission of the defect, seems to differ in no way from the earlier stock

But now let us inquire as to where all this leads Without entering into a discussion of just what, serologically, is taking place in the body or in the germ of fetuses borne by the lens treated mothers, the point I wish to emphasize is that a certain specific effect has been produced, and, what is of greater moment, once the condition is established it may be not merely transmitted, but inherited Whether the lens of the uterine young is first changed and then in turn induces a change in the lens producing antecedents in the germ-cells of these young, or whether the specific antibody simultaneously affects the eyes and the germ cells of the young is not clear In any event it is evident that there is some constitutional identity between the

substance of the mature organ in question and the material antecedents of such an organ as it exists in the germ

Biologically considered, the most significant fact is that specific antibodies can induce specific modifications in the germ cell. Whether these antibodies are transmitted from the mother s blood or engendered in that of the young would seem to be of secondary importance It stands to reason that antibodies originated in an animal s own blood will modify germinal factors if corresponding antibodies introduced from without can accomplish this

The whole question as to how important such a fact may be in contributing to an understanding of the causes of the germinal changes in organisms in general which lead to variation and evolution hinges on the question of whether changes in an animal s tissue will induce the formation of antibodies or kindred active substances in its own body We have been steadily accumulating evidence that such reactions do occur

In our own laboratory, for example, after many attempts we have succeeded in securing a defective-eyed young rabbit from a mother of normal stock by injecting her repeatedly with pulped rabbit lens before and during pregnancy Since the young rabbit in question has both eyes badly affected there can be no question that a rabbit can build antibodies against rabbit tissue which are as effective as those engendered in a foreign species such as the fowl We have likewise found it relatively easy to secure spermatoxins by directly injecting rabbits, both male and female with rabbit spermatozoa Moreover, a given male will develop antibodies against his own spermatozoa if he is injected intravenously with the latter

We are also securing evidence that serologic reactions induced in the fetus through operations on the mother are not mere passive transmissions, but may become actively participated in by the tissues of the fetus. For example, female rabbits sensitized with typhoid vaccine followed by living typhoid germs may transmit to their young and even to their grand descendants the ability to agglutinate typhoid bacilli in serum diluted from 60 to 160 times From the standpoint of heredity we have no reason so far for maintaining that this is anything but placental transmission, though we are going to practice immunization generation after generation for a number of generations to determine if a truly hereditary immunity will be established However, facts have come to light which show that there is more concerned in the operation than a mere transfer of antibodies from mother to

fetus For instance, the blood of young shortly after birth may show a higher titer than that of the mother Again, after two or three months of development the young of certain of the sensitized mothers have shown a rather sudden rise in titer, much above that of the mothers In such cases it would seem that some mechanism in the young rabbit itself is constructing antibodies which supplement those passively derived from the mother Possibly in the process of development some organ important in such reactions just came into functioning If this is true further experiments may throw some light on the perplexing question of the source or sources of the antibodies in an animal After a few weeks, in such cases, the titer drops back again In still another set of experiments we found that young from a sensitized mother, when nursed by a normal untreated mother, retained a fairly high titer for several months and even showed the rise of titer mentioned On the other hand, young of an untreated mother when nursed by a sensitized mother acquired a fairly high titer from the milk of the foster mother but lost it rapidly after weaning time Thus there are evidently constitutional factors operative in the young which have acquired their immunity through the placenta which are absent in the young whose antibodies were conveyed through food

That changes in the blood serum may be caused by changed conditions in the tissues is further attested by many facts For example, in pregnancy, the newly forming placenta may set free cells or cell-products which, sometimes at least, cause changes in the blood serum of the mother, though the exact nature of these changes is in dispute Romer, using the complement fixation technique, found that the serum of adult human beings may possess antibodies for their own lens proteins Bradley and Sansum, employing anaphylactic reactions, found that guinea pigs injected with guinea pig tissue-proteins (liver, heart, muscle, testicle, kidney) develop immunity reactions Again during the late war, the type of toxic action to which anaphylactic shock conforms was found to exist after extensive injury of the soft tissues It resulted apparently from the absorption of poisonous substances of tissue origin into the circulation. In fact, various cells and tissues when injured liberate such poisons, and even blood in clotting is known to acquire a transient toxicity of this type

With facts such as these before us, is it not a rational hypothesis *to assume that changes in various parts of a body* may on occasion influence the representatives of such parts in the germ-cells borne by that body? This appears all the more probable when we recall the

facts learned from a study of precipitins and of anaphylaxis that each species of animal has a thread of fundamental similarity underlying the proteins of all its tissues There is no reason to suppose that germinal tissue forms an exception. The further fact that homologous tissues, though existing in different species of animals possess similar chemical characteristics shows that to get an effect there need not be absolute chemical identity between the substance of such a tissue as the lens and the germinal constituents of which it is the expression. And if this is true for lens why not for other tissues?

The blood serum of any organism with blood thus affords a means of conveying the effects of changes in a parental organ to the germ cell which contains the antecedent of such an organ As long as there is little change in the somatic element its germinal correlative would presumably remain constant, but any alternations of the soma which give rise to the formation of anti bodies or other active agents particularly if long continued, might induce changes in the germ Such a hypothesis would seem to be plausible at least in accounting for degenerative changes such as the deterioration of eyes in such forms as the mole, or in fact, in the formation of vestigial organs in general

On the other hand, there is no reason to infer that changes induced in the blood serum may not also be instrumental in leading to progressive as well as regressive evolution If we may have germinally destructive constituents engendered in the blood there is no valid reason for supposing that we may not also have constructive ones When we learn more about what initiates and promotes growth in a part through exercise, or what causes hypertrophy of an organ, we may likewise find how corresponding germinal antecedents of that part may be enhanced. Until such time we shall probably remain in the dark regarding the mechanism of progressive germinal changes As already indicated in the hormones and chalones we have a wonderful series of secretions normally circulating in the blood and maintaining general physiological equilibrium That reciprocal stimulations of various organs occur by this means is a well-established fact. Hypertrophy or atrophy of an endocrine gland may produce pronounced effects in the furthermost reaches of the body Again we may inquire, is it reasonable to suppose that the germinal tissues will be inviolate to all this ebb and flow of chemical influence? Should we not expect specific reactions or selections here no less surely than in other tissues? Destruction of the pars buccalis of the hypophysis in the frog tadpole will cause profound alteration in other endocrine organs such as the

adrenals and thyroids, will retard the growth rate, render the entire organism albinous, and produce in the individual pigment cells a condition of sustained contraction Shall we conclude that such a far reaching influence as this, particularly in a developing organism, will pass the germ cells by unscathed?

Similarly, growth in man is known to be controlled by a pituitary secretion that is carried by the blood to the various organs The normal development of secondary sexual characters is determined by products from the testes or ovaries, and the activities of the generative organs themselves are intimately associated with the functioning of the adrenal and other glands The periods of ovulation are inhibited by secretions from the corpus luteum, lactation is incited by products of the corpus luteum, the involuting uterus and the placenta, the carbohydrate metabolism in the liver and even in the most distant muscles is profoundly influenced by substances formed in the pancreas, the pancreas, liver, and intestinal glands are set to secreting through the stimulus of a product formed in the duodenal and jejunal mucosae And still others of such remarkable interrelations can be cited

Truly one may pronounce that social complex of reciprocating individuals termed cells which make up an organism, 'members one of another" And with all of these co operative activities of the various parts of the body it is inconceivable to me, at least, that the germ-cells, bathed in the same fluid, nourished with the same food stand wholly apart

May we not surmise then that as regards inheritance and evolution, Lamarck was not wholly in error when he stressed the importance of use and disuse of a part, or of modifications due to environmental change, in altering the course of the hereditary stream, particularly if we conceive of these influences as being prolonged, possibly over many generations? Have we not in the serological mechanism of the body of animals an adequate means for the incitement of the germinal changes which underly certain aspects of evolution?

RECENT EXPERIMENTS BELIEVED TO FAVOR THE LAMARCKIAN THEORY

Guyer and Smith, in continuation of their earlier program report that they have induced hereditary changes in the eyes of fetuses by a much simpler method than that described above By simply destroy

ing the lens of the living female rabbit by "needling" *in situ*, anti lens serum has been produced in the blood of these animals This material was as effective in preventing the development of lenses in some of the fetuses of these mothers as was the material produced by more elaborate serological methods Also the effects seem to be inherited in the same way as in the former experiments It should be noted that Guyer is very cautious in his statements and makes no claim that his work demonstrates the inheritance of acquired characters He realizes that the same specific material that is supposed to inhibit the development of eye structures in the young fetus might readily at the same time exert a specific influence upon the genes or factors for eye structures in the primordial germ cells that live contemporaneously with the somatic structures Thus two generations might be affected simultaneously—a case of parallel induction

Every important experiment in science becomes the target of attack, and the experiments of Guyer and Smith are no exception Bagg and Hanson and Little have performed some very interesting experiments on the effects of radium emanations and of X rays on mammalian germ cells and Stockard has used alcohol in the same way All of these workers show that eye defects, especially lens defects, are found most commonly, occurring sometimes in the entire absence of other observable defects It would seem, then, that eye defects are far from being specific, and they may not be specific in the experiments of Guyer and Smith There is no question but that the eye is the most susceptible part of the organism and that eye defects can be induced in vertebrates by almost any kind of inhibiting agent It was only when Guyer used the lens material, however, that he got lens defects, for when he used sera developed from other tissues no effect upon the lens was noted But no effect upon any other tissue was noted, seeming to show that no effective antigens of any sort were formed It is impossible at the present writing to predict what will be the final bearing of Guyer's and Smith s very significant experiments upon the problem of the inheritance of acquired characters

Griffith and Detlefson have recently reported some experiments upon mice that at first seemed almost crucial for our problem Rats were reared for several months in cages placed upon rotating tables They became adapted to the rotating condition to such an extent that when the rotation was stopped they seemed upset, showing signs of nystagmus (dizziness) and other symptoms of a changed physiological condition Some of the young born outside the cages showed irregular

ties in their gait and other signs of nystagmus Moreover, the young of parents rotated to the left showed different effects from those of parents rotated to the right The condition is said to have been inherited for several generations Detlefson, however, noted that the whirled rats and their offspring showed frequent pathological sequelae such as discharges from the ears, and is now inclined to wonder 'whether Griffith has not merely presented us with numerous specimens of some vertebral disease" The implication is that the disease once started might be passed on to future generations by infection It is generally understood that Detlefson has been repeating these experiments upon the Wistar Institute standard white rats, and that his results are so far negative

And thus stands the problem today It is no more settled than it was fifty years ago but most of us are growing to be a little pessimistic about the whole matter

CHAPTER XXXII

OTHER POSSIBLE GUIDING FACTORS

Orthogenesis Geneticists as a rule feel that natural selection is the only guiding factor needed to account for the adaptive features of evolution They are inclined to be skeptical about the definiteness of the pathways of change that have been so strongly emphasized by palaeontologists and others T H Morgan at one time expressed the view that most of the beautifully precise orthogenetic pedigrees such as that of the horse family for example might be made up by selecting only those fossil forms that fitted well into the progressive series and ignoring those that did not fit so well He showed that one could make out a very pretty phylogeny of the spear heads displayed in museums in which each type leads to another type and all are capable of arrangement into a few orthogenetic series Since such a series is merely an artificial arrangement without phylogenetic significance the same might also to some extent be true for the orthogenetic series of the palaeontologist Some geneticists are inclined to think that the evolution of the horse family for example had been much less definitely directed than it is commonly supposed to be In each period there existed numerous less progressive types and many aberrant species as well as those that seem to follow the more direct lines leading to the modern horses In other words much of the definiteness of direction is the result of focusing attention upon a few of the types that make a good series and ignoring the ones that are not in line This criticism is possibly too iconoclastic There surely is in the horse pedigree some definiteness of trend amidst a flux of indefiniteness Hence the problem of explaining this residual definiteness still remains

In recent years one of the staunch supporters of the reality of orthogenesis has been *H F Osborn* His most striking material perhaps consists of the fossil pedigrees of the *Titanotheres* a group of extinct ungulates somewhat resembling the modern rhinoceros They appeared relatively early in the evolution of mammals, and attained giant proportions great abundance and wide distribution before becoming extinct at the close of the Oligocene period Though the titanotheres started as small creatures about the size of terriers they reached almost the dimensions of elephants near the close of their career One of

their outstanding peculiarities consists of a unique type of horn on the tip of the nose, a horn branching at the base and diverging laterally into two flat prongs Osborn distinguishes at least four divergent lines of evolution among these mammals Line I retained the front teeth (incisors) and remained heavy bodied Line II lost the incisors and became longer limbed, lighter bodied, speedier, and went in for grazing In neither of these lines did the horns grow very large Line III, the first of the large-horned lines, lost the incisors and remained relatively small bodied Line IV, to which the giant *Bro totherium* belongs, retained the incisors, grew extremely bulky, and went in for slow, leisurely browsing

In all these four lines that are known to have separated early and to have remained genetically independent throughout their careers, the evolution of the horns has run parallel courses All four lines started hornless, each developed horns independently, and the steps in horn evolution ran the same course in all the four lines, going somewhat farther in the larger types than in the smaller In the last sur viving representatives of all four lines the horns had reached the same characteristic form, being attached to the same bones of the skull and having a shape quite unlike that known for any other group of mam mals

The inferences that have been drawn from this situation are as follows The original ancestral titanotheres must have had something in the germ plasm that was predestined to vary along certain definite lines and to produce certain definite structures, in spite of any differ ences in environment or habits of the different lines of descendants The horns were compelled to appear at a certain stage in the evolution of each of the four lines, though they may have had little or no adap tive value Osborn has no very satisfactory theory as to the mechan ism involved in this remarkable orthogenesis, but Julian Huxley has offered a purely physiological explanation of horn evolution in titano theres, an explanation that may apply equally well to many other cases He has discovered that in horned animals in general, the larger the individual is, the larger are the horns in proportion to the body size Now, as is true of most phylogenetic series, there was a steady increase in size in all four lines of titanotheres Thus the earliest titanotheres were too small to have horns at all, the first horned types were of moderate size, the most elaborately horned types were the giant end products of each of the four lines, and especially was this the case for the great *Brontotherium*

If, then, as seems to be the case horn evolution is merely a secondary and purely incidental consequence of increase in size, we may well ask why increase in size goes on so steadily Is this not an orthogenetic process itself? But increase in size may be guided by natural selection without the aid of other factors for increase in size confers a personal advantage upon the individual though it may in the end be damaging to the race Thus a larger bull in a herd will be stronger and win more mates thus tending to pass on the genes for larger size to descendants

Darwin would have called the case of horns in titanotheres an example of correlated variation and would have said that here we have an instance of some adaptive characteristic such as body size carrying along with it a variable character that may have little or no adaptive value Thus this classic case of orthogenesis would be explained satisfactorily as the result of correlated variation and natural selection without dragging in any inner guiding principle

In view of these and many other facts it seems advisable, for the present at least to say nothing further about orthogenesis. No very good case of orthogenesis has been presented that cannot be explained as well by natural selection as in any other way that has been suggested So little do geneticists as a group think of orthogenesis as a possible guiding factor in evolution that most textbooks of genetics do not mention the word even in the index Orthogenesis is at present a concept that belongs rather to the philosophy of evolution than to the science of genetics

Vitalistic theories — All theories of evolution based on known mechanisms are considered as mechanistic and belong in the realm of science but there are some theories known as "vitalistic" that belong more to the realm of philosophy than to that of science Several of these theories deal with some kind of immaterial force or forces that are believed to guide the course of evolution Bergson's *élan vital*, or vital urge, is one of these immaterial forces. This force is believed to be practically synonymous with life itself It is that property of life that gives to it a drive forward, a tendency to grow, multiply, and adapt itself In a sense, it is a sort of inarticulate purpose residing in the living substance itself This protoplasmic purpose continually expresses itself in adaptive development and adaptive behavior It realizes itself most completely as mind, purpose and reason in higher organisms, but its essence is present in even the lowest organisms and in the youngest stages of the individual It guides the course of in

dividual development, each step of which seems to be in preparation for the next, as though taken in anticipation of it

The reader may well revolt against the introduction of speculations of this sort into a treatment of the mechanism of evolution, but if such a concept as *élan vital* does nothing more than to serve as a contrast with the more tangible and verifiable mechanisms of evolution we have previously dealt with, it will have justified the space given to it

CHAPTER XXXIII

DIVIDING FACTORS ISOLATION

Introductory — As has so often been pointed out, one of the most conspicuous features of animal and plant life is their subdivision into a multiplicity of taxonomic divisions such as phyla classes, orders families genera species and varieties In any one particular environment one finds large numbers of representatives of numerous groups a fact that seems to imply that the environment alone is an insufficient cause of multiplicity of forms, for if it were, a single environment should produce only one type and the same environment should always produce the same type Also, it is very frequently true that differences distinguishing two allied species are not obviously adapted to the differences in the environment but are rather trivial characters such as color markings proportions of parts, etc. Hence we cannot explain the multiplicity of types on purely environmental grounds

Our studies of geographic distribution as evidences of evolution have emphasized the fact that mere geographic isolation, apart from climatic differences involved, are invariably accompanied by various degrees of divergence between the isolated members of the same group the divergence sometimes being so great as to constitute family distinctions more frequently generic, and very commonly specific or varietal The degree of divergence parallels closely the degree of completeness of isolation and the extent of time during which isolation has been operative

Opinions among authorities differ as to whether mutations and selection alone are sufficient to account for the multiplicity of forms and their distribution in space Some of the more extreme neo-Darwinians on the one hand, are inclined to believe that natural selection is sufficient unto itself to explain all of the observed facts Extreme advocates of the isolation theory, on the other hand, look upon isolation as an absolutely essential mechanism for species formation nearly as important as natural selection itself The writer believes that isolation is an absolutely essential part of any complete explanation of evolution but that it is a subsidiary factor often working in such intimate relation with natural selection and Mendelian heredity as to be almost inseparable from them

"Isolation" used in the broadest sense —The term "isolation" is a somewhat unfortunate one to use for the type of factor we are here dealing with It implies physical separation in the geographical sense whereas there are very many types of isolation not at all based upon spatial separation In the broadest sense any factor may be said to play an isolating rôle if it interferes with free interbreeding among all the members of a species Completely free interbreeding within the entire range of a species would result sooner or later in an equal distribution among the individuals of the species of all viable hereditary changes Unless something were to interfere with free interbreeding within the species it would remain indefinitely one evolving unit and would not subdivide

But there are a great many ways in which free interbreeding may be interfered with Among the most important isolating agents are the following (*a*) geographic isolation involving the setting up of geographic barriers between subdivisions of the species (*b*) sheer distance apart of extreme sections of a species covering a large territory, not involving any other isolation agencies (*c*) climatic differences within the range of the species (*d*) physical differences in the environment, such as differences in water soil sunlight elevation of land, etc , (*e*) biotic differences in the environment involving the presence of various other animals and plants within the range of the species in question (*f*) reproductive differences among individuals due to genetic changes that alter the developmental rhythm or the copulatory apparatus, bringing about assortative mating and (*g*) psychic differences that result in what is known as clannishness among human beings according to which changed forms tend to mate with their own kind more readily than with others

All these and doubtless other agencies promote isolation of small or large groups within the species and tend to split the species up into a number of more or less separately breeding groups

Isolation and inbreeding —One of the inevitable consequences of the isolation of a relatively small group from the main body of the species is inbreeding more or less close In extreme cases of geographic isolation a new race may be derived from one pair of individuals The offspring of such a pair, if they breed at all must breed together, and for successive generations there will be much close inbreeding Geneticists have demonstrated that continuous inbreeding results in a decrease of heterozygous and an increase in homozygous individuals Now, even if no new mutations occurred nor any selection of types due

to changed environmental requirements took place, such an isolated group would already have a good start toward becoming a separate race or species because of the effects of inbreeding.

Isolation and selection. Divergence may also be promoted by selection. When an isolated group of a species finds itself in a different environment from that of the parent stock, selection may tend to preserve individuals with either the dominant or the recessive of any unit character or any combination of these that may happen to be more advantageous than others under the changed conditions of life. In this way some genes may be entirely eliminated from a stock, thus increasing the genetic differences between the parent species and their isolated derivatives. If, for example, a small section of a species were to become isolated in a region where the available food was quite different from that in the main range of the species, some of the individuals, because of favorable combinations of unit characters, might immediately find themselves better equipped to cope with the new food conditions than others. These adapted to the new food conditions would live and breed together and would tend to become homozygous for the various characters that favored their survival under the new conditions.

THE VARIOUS CATEGORIES OF ISOLATION

a) **Geographic Isolation.**—Taxonomists who have studied and plotted the distribution of species of animals and plants are most familiar with the effects of geographic isolation. They consider that one of the most certain facts of nature is that isolation is always accompanied by marked differences between the isolated branches of a species. The late *David Starr Jordan*,[1] a leading student of geographic isolation in America, discusses the subject in a very illuminating fashion:

"It is now nearly forty years since Moritz Wagner (1868) first made it clear that geographic isolation (*räumliche Sonderung*) was a factor or condition in the formation of every species, race, or tribe of animal or plant we know on the face of the earth. This conclusion is accepted as almost self-evident by every competent student of species or of the geographical distribution of species. But to those who approach the subject of evolution from some other side the principles set forth by Wagner seem less clear. They have never been confuted, scarcely ever attacked, so far as the present writer remem-

[1] *Science*, N.S., Vol. XXII (1905).

bers, but in the literature of evolution of the present day they have been almost universally ignored Nowadays much of our discussion turns on the question of whether or not minute favorable variations would enable their possessors little by little to gain on the parent stock, so that a new race would be established side by side with the old or on whether a wide fluctuation or mutation would give rise to a new species which would hold its own in competition with the parent In theory, either of these conditions might exist In fact, both of them are virtually unknown In nature a closely related distinct species is not often quite side by side with the old It is simply next to it geographically or geologically speaking and the degree of distinction almost always bears a relation to the importance or the permanence of the barrier separating the supposed new stock from the parent stock

"A flood of light may be thrown on the theoretical problem of the origin of species by the study of the probable actual origin of species with which we are familiar or of which the actual history or the actual ramifications may in some degree be traced

'In regions broken by few barriers, migration and interbreeding being allowed, we find widely distributed species homogeneous in their character, the members showing individual fluctuation and climatic effects, but remaining uniform in most regards all representatives slowly changing together in the process of adaptation by natural selection In regions broken by barriers which isolate groups of individuals we find a great number of related species though in most cases the same region contains a smaller number of genera or families In other words the new species will be formed conditioned on isolation, though these same barriers may shut out altogether forms of life which would invade the open district

"Given any species in any region, the nearest related species is not likely to be found in the same region nor in a remote region, but in a neighboring district separated from the first by a barrier of some sort

'Doubtless wide fluctuations or mutations in every species are more common than we suppose With free access to the mass of the species, these are lost through interbreeding Isolate them as in a garden or an enclosure or on an island, and these may be continued and intensified to form new species or races Any horticulturist will illustrate this

"In all these and in similar cases we may confidently affirm The adaptive characters a species may present are due to natural selection

or are developed in connection with the demands of competition The characters non adaptive which chiefly distinguish species do not result from natural selection but from some form of geographical isolation and the segregation of individuals resulting from it "

J T Gulick another exponent of the efficacy of geographic isolation in species forming has offered in evidence of his views facts about the distribution of Hawaiian land snails In the island of Oahu, for example the volcanic ridges have been eroded out into a series of isolated valleys in the bottoms of which grows abundant vegetation while on the highlands there is little but barren rock The climatic conditions of all the numerous valleys are the same, but, remarkably enough each variety of snail is confined not only to one island, but to a definite valley on an island The degree of difference, moreover, between varieties is in proportion to the distance that separates them Gulick claimed that he was able to estimate the degree of divergence between the snails of any two valleys by measuring the number of miles that lay between them Gulick s findings have been extensively corroborated by recent explorations on the snails of other oceanic islands by Crampton

An interesting type of isolation that hardly can be termed geographic yet is essentially equivalent to the latter in its effects is found in connection with the extensive group of lice (Mallophaga) that live their whole lives buried among the feathers of birds or the hair of mammals These animals cannot fly and are quite effectively isolated for life upon a particular bird They do however, during the intimate period of nesting pass from parent to offspring, so that they may be said to be isolated upon definite genetic lines In the case, especially, of birds like the eagle a bird of long life and monogamous habits, the parasite becomes as isolated as might be a race on a small island The result is that sometimes the lice of a single bird and its offspring are of quite a distinct variety, which has become fixed by inbreeding until a high degree of uniformity has been attained Such an isolated variety may be almost as distinct as a true species Obviously in this case as in others isolation must have had a real effect upon species forming quite apart from natural selection, except in so far as the unfit variants have not survived

Populations of lakes and ponds—Just as islands of land in seas of water serve to isolate terrestrial forms, so islands of water in seas of land if we may be pardoned the expression, just as effectively isolate aquatic organisms Thus isolated ponds and lakes commonly harbor

species of fishes and other aquatic types different from those found anywhere else in the world As a young naturalist I became interested in the fauna of Lake Maxinkuckee in Indiana a spring fed lake that is practically cut off from communication with other bodies of water While I was there Evermann and Clark were making a very exhaustive biological survey of this lake and discovered a surprising number of species peculiar to this one body of water Hundreds of similar situations doubtless exist all over the world

Populations of mountains —Certain types of plants characteristic of high mountains are commonly isolated from others of their kind by valleys and by discontinuities in mountain chains Patches of lowland thus isolate patches of mountains and the result is as one might expect that each isolated high mountain chain has its own local races or sub species of plants

b) Isolation due to sheer distance apart —If a species ranges all over a wide extent of territory which is unbroken by barriers there may be isolation because of the great distances between extreme outlying sections of the range Students of the evolution of great groups of mammals for example consider that very large continental bodies must have been the main theaters of evolution because smaller land bodies would not permit of diversification of types through isolation *Thus the body of land known as Holarctica embodying Northern* Asia Northern Europe and Northern America is believed to have been the principal theater of mammalian evolution In this great area there was plenty of room for groups to become spatially isolated even without positive barriers and in this area it is believed that all the original divergences occurred that gave origin to the principle sub divisions of mammals Migration along many southern routes has subsequently more completely isolated and fixed the various mammalian faunas of Southern Asia Australasia Africa and South America

The original divergences resulting from mere spatial isolation would be the result of the inability of the most widely separated sections of a species to interbreed If they failed to interbreed mutations occurring in one section would remain in that section and those occurring in another section would likewise remain in that section Thus two independent evolutions would go on and local races or varieties would result that in time would become separate species especially if *they subsequently migrated along different* paths to different isolated regions

A good example of geographic races or sub-species arising in an extensive area unbroken by effective barriers is seen in the case of the wrens of South America Wrens are found practically all over that continent, but those in one region differ from those in others in color patterns, size proportions and habits In the absence of barriers all these local races grade into each other In certain regions however, that happen to be more than usually isolated as when a high mountain range intervenes transitional forms are missing The point is, however, that whether barriers are present or not, sheer distance apart tends to produce local races

c) Climatic isolation —There often occur distinct and more or less abrupt climatic differences within the range of a species which may act as barriers to migration or involve different adaptive changes on the part of individuals living under these different climatic conditions Thus without the presence of any geographic barriers, a species may split up into a northern and a southern race or sub-species that are genetically distinct neither thriving in the territory occupied by the other Similarly in the oceans there exist rather abrupt differences in temperatures that act as effective barriers The waters north and south of Cape Cod for example have almost entirely different faunas The reason for this is that the shore-line north of Cape Cod is made cold by the Labrador Current and that south of the Cape is more influenced by the warm Gulf Stream Species north of the Cape and south of the Cape are almost as distinct as if they belonged to different oceans

d) Biotic isolation —The territory occupied by any species of animal or plant is always occupied by many other species Some of these associated species may occupy one part, some another part of the range of the species in question Now each species affects all the other species with which it is spatially associated, each species is a part of the biotic environment of all the others If, then, the biotic environment varies within the range of the species, the pressure of selection will vary also certain characters or combinations of characters being more favorable for one biotic environment than another This being the case, groups in different biotic environments will tend to be isolated from one another and will diverge in both adaptive and non adaptive directions

e) Reproductive isolation —The simplest type of reproductive isolation is one that involves changes due to mutations in the copulatory organs In some insects for example, the copulatory organs are con

structed on the lock and key principle, only a certain pattern of key fitting a certain pattern of lock Any change in the pattern of these organs prevents the members of the changed type from breeding with the unchanged individuals and forces them to breed only with those that have changed in appropriate fashion Fortunately, when a change occurs, it usually affects both sexes in such a manner that males and females of the changed type can mate No actual observations of new races arising in this way have been observed but there are numerous cases of closely allied species that are intersterile because of slight differences in the pattern of their copulatory organs

One of the most effective means of bringing about reproductive isolation is a change in the developmental rhythm of a section of a species If, for example, some plants of a species flower earlier or later in the season than others they are able to interbreed only with those having the same developmental rate If such a difference in developmental rate be genetic a real isolation of these different races will be effected and further divergence will follow A similar situation also occurs among animals The genus *Cicada*, commonly called locusts," has probably split up into numerous species as the result of genetic modifications in the lengths of their life cycles Whereas there are only slight morphological differences among the species of *Cicada*, there are pronounced differences in the lengths of the larval periods In the "seventeen year locusts," for example, the larval life under ground is over sixteen years As a result of this, only once in seventeen years do the adult broods appear above ground They must, there fore, mate only with members of their own brood in the same territory Similarly, there are fourteen year, eleven year, nine year, and seven year species, etc, each of which is reproductively isolated in any territory from all others, for rarely do two species reach maturity in *any region during the same season Even in one species scattered* over a wide expanse of territory different broods appear one or two seasons apart, and this tends to isolate sections of the present species from one another and will doubtless produce further splitting up of species as time goes on Doubtless many other situations similar to these, but less extreme, exist among both animals and plants That changes in developmental rate do exist within a species and have a genetic basis, is attested by the fact that many early and late fruiting varieties of domestic plants have been isolated, some of which are more suitable for a long southern growing season and others for the relatively short northern season

f) Psychic isolation —A synonym for psychic isolation is "clannishness Even among lower animals there appears to be a well defined tendency for like to mate with like 'Assortative mating is another term commonly used to denote this tendency In man conventional mating is highly assortative Sporadic sex unions between members of radically different races not uncommonly occur, but formal marriages are rare between members of distinct races. This tends to preserve a residue of racial separateness that would long ago have disappeared except for clannishness

Examples of this sort of thing in the animal world are not far to seek *Beebe* cites the interesting case of two color phases of gannets occupying an old volcanic crater together but keeping absolutely separate in their breeding activities The main gannet population consisted of white birds but out toward the center of the crater there was a small compact and unmixed clump of sooty birds which could doubtless have readily interbred with whites but never did so preferring their own kind

It was Darwin I believe who described the case of droves of wild horses of the Caucasus region that were all of one color in a drove One drove would be all bays another all blacks another all chestnuts Apparently these droves consisted of closely related individuals that preferred to mate only with their own kind Long-continued reproductive isolation of this sort might readily bring about the origin of separate races and in time separate species

Most of the types of isolation briefly discussed above are somewhat hypothetical in that they are derived from observations of nature after the event as it were Very little real experimental work has been done in this field except in connection with inbreeding and selection In animal and plant breeding man merely isolates a pair of individuals usually beginning with a brother and sister, and begins an inbred line selecting usually the most promising individuals for further inbreeding In this way excellent homozygous strains are produced that have peculiar characteristics of their own unlike those of any other strain Hence artificial inbreeding and selection is a kind of reproductive isolation having the same effects as has extreme isolation in nature There can be no doubt, then, that the various types of isolation have the effects attributed to them namely, those of splitting up species and of preserving incipient races from being swamped out by back-crossing with the parent stock

PART IV

EUGENICS

CHAPTER XXXIV

INTRODUCTION TO EUGENICS

Definitions of eugenics.—"Eugenics" is a term coined by Sir Francis Galton in 1883, and was defined by him as the "study of agencies under social control that may improve or impair the racial qualities of future generations, either physically or mentally." More specifically, eugenics is that science which deals with human variation and heredity and attempts to improve the human stock by selective breeding according to the known laws of genetics. In still different words, eugenics may be defined as the application of genetics to man with the hope that man might control his own evolution and save himself from racial degeneration.

Eugenists feel that many of the ills of the world might be cured by an application of eugenic measures. "We must endeavor," says a president of the American Eugenic Society, "to show that eugenics supplies the most effective and permanent solution to the problems that have been so ineffectively dealt with hitherto by physicians, pub

This rather sanguine statement is echoed in somewhat different words by Jennings. "The troubles of the world, and the remedy of these troubles lie fundamentally in the diverse hereditary constitutions of human beings. Some men are strong, healthy, wise, virtuous. Others are weak, foolish, diseased, immoral, criminal, and it is these that cause the troubles of the world. Laws, customs, education, material surroundings, are the creations of men and reflect their fundamental nature. To attempt to correct these things is merely to treat superficial symptoms. To go to the root of the troubles a better breed of men must be produced, one that shall not contain the inferior types. When a better breed has taken over the business of the world laws, customs, education, material conditions will take care of themselves. Good men, wise men, will make a good world."

In a somewhat roundabout way we have thus defined eugenics by stating the views of some of the leading advocates of eugenics.

The scope of eugenics —The range of subjects usually considered within the realm of interest of students of eugenics may well be stated by quoting from the prospectus published in connection with the Second International Congress of Eugenics that met in New York in September, 1921 The Congress met in four sections each of which devoted itself to one of the major fields of eugenics The four sections are described as follows

"I. In the first section of the Congress will be presented, on the one hand the results of research in the domain of pure genetics in animals and plants and on the other studies of *human heredity* The application to man of the laws of heredity and the physiology of reproduction as worked out on some of the lower animals will also be presented

"II The second section will consider factors which influence the *human family*, and their control, the relation of fecundity of different strains and families and the question of social and legal control of such fecundity, also the differential mortality of the eugenically superior and inferior stocks and the influence upon such mortality of special factors, such as war and epidemic and endemic diseases. First in importance among the agencies for the improvement of the race is the marriage relation with its antecedent mate selection Such selection should be influenced by natural sentiment and by a knowledge of the significant family traits of the proposed consorts and of the method of inheritance of these traits In this connection will be brought forward facts of improved and of unimproved families and of the persistence, generation after generation, of the best as well as the worst characteristics

"III The third section will concern itself with the topic of *human racial* differences with the sharp distinction between racial characteristics and the unnatural associations often created by political and national boundaries In this connection will be considered the facts of the migrations of races the influence of racial characteristics on human history, the teachings of the past with bearings on the policies of the future Certain prejudices directed toward existing races will be removed when allowance is made for the influence of their social and educational environment, and their fundamentally sound and strong racial characteristics are brought to light On the other hand limits to development of certain races and the inalterability through education and environment of the fundamental characteristics of certain stocks will be considered Finally the advantages and disadvantages

of the mingling of races, of unions which have proved to be fateful to social progress, should be discussed In this section will be presented the results of researches upon racial mixtures in relation to human history Also the topics of racial differences in disease and psychology will be taken up The history of race migrations and their influence on the fate of nations, especially modern immigration should be set forth

"IV The fourth section will discuss eugenics in relation to the state, to society and to education It will include studies on certain practical applications of eugenic research and on the value of such findings to morals, to education, to history, and to the various social problems and movements of the day In this section will be considered the bearing of genetical discoveries upon the question of human differences and upon the desirability of adjusting the educational program to such differences Here will be considered the importance of family history studies for the better understanding and treatment of various types of hospital cases and those requiring custodial care The bearings of genetics on sociology, economics and the fate of nations may be considered in this section "

This outline of the program of the Eugenics Congress shows clearly that eugenics is a broadly conceived subject It is not merely a branch of genetics, but has intimate relations with sociology, economics, legal science, political science, the scientific study of crime and delinquency, medical science, and education

The aims and ideals of eugenics —The hopes and ideals of eugenists are well expressed in the closing paragraph of the address of the president of the last International Congress of Eugenics, Major Leonard Darwin, an illustrious grandson of Charles Darwin

"Eugenics aims at increasing the rate of multiplication of stocks above the average in heritable qualities, and at decreasing that rate in the case of stocks below that average But if the banner under which we are to fight should only have inscribed on it some such an and definition of policy as this, our defeat would be certain We must prove that we are under the guidance of a noble ideal We of this generation are responsible for the prod[illegible]

genic ideal. The belief that man has been slowly developed from some ape-like progenitor came toward the close of the last century to be near

ly universally held by thoughtful persons this belief gave rise to a new hope that this upward march of mankind might be continued in the future, and out of this new hope sprang the eugenic ideal This growing understanding of the past history of the world has led us to see that, if we are to imitate Nature in her methods, we must be content to advance by a long succession of small steps, just as rain falling in drops on the earth has slowly carved out mighty valleys in the hardest rocks Without constructing wild Utopias, we must be content if some little racial progress can be ensured as each generation succeeds another, for to work in this spirit is to work in harmony with the knowledge which gave birth to the eugenic ideal Progress on eugenic lines will make mankind continually nobler, happier, and healthier, whilst those who imagine that our sole aim is to make man a stronger animal or a better beast of burden are utterly ignorant of the meaning of the eugenic ideal But science, whilst giving us good grounds for hope, also issues a grave warning concerning the danger of national deterioration resulting from the unchecked multiplication of inferior types In the past many nations of the first rank, when apparently advancing without check on the path of prosperity, have begun to decay from unseen causes, and have in time so fallen from their high estate as to cease to count as factors making for progress A determination that such a downfall shall not be the fate of his nation is a sentiment felt by every man who is animated by the eugenic ideal an ideal to be followed like a flag in battle without thought of personal gain '

Methods of research in eugenics —The programs of research in the field of eugenics, as broadly stated in the four paragraphs outlining the four sections of the Congress cover so many interests and impinge upon so many fields of research that have little, if any, bearing on the subject matter of the present course that we shall limit our discussion of methods to those applicable to the study of human heredity The chief methods of discovering the facts about human heredity are as follows

a) The pedigree method —According to this method, a study is made of the history of human matings, including all generations simultaneously living and the records of those recently deceased The method of the experimental breeder cannot be used, but each fertile human mating is looked upon as an experiment in genetics, the results of which we may record and from which we may draw conclusions

b) The statistical method—A great deal can be learned about the heredity of fluctuating and graduated differences such as those of height weight, longevity, etc , by determining the degree of correlation that exists between a large group of parents and a large group of offspring Galton and his successor Karl Pearson are the chief exponents of this method

c) The twin method—This method is quite distinct from either of those just listed though it may use statistical methods Many facts may be determined by the use of one egg (monozygotic) and two-egg (dizygotic) twins about what is inherited in man and what characters are commonly modified by the environment

A separate chapter will be devoted to a discussion of each of these methods and the contributions to our knowledge of human heredity that have accrued from their use

CHAPTER XXXV

HUMAN HEREDITY AS REVEALED BY PEDIGREES

Weaknesses of the pedigree method.—The older type of pedigree study involved the collecting of pedigrees made out by persons untrained in genetics and dealing with individuals in their own family connections. Questionnaires were sent out to large numbers of individuals asking them to give data as to characteristics of their ancestors and other relatives. Much of the material thus collected depended upon the vague memories of individuals about the characteristics of long dead ancestors or of relatives in collateral lines. The low degree of reliability of such data makes conclusions therefrom almost useless. Considerably more reliable data were obtained by field workers who actually observed individuals belonging to four, in extreme cases five generations all living simultaneously. The reliability of such data depends upon the training and scientific aptitude of the field worker. Fortunately, there has developed in recent years a new profession, that of eugenic field worker, and there are not a few very capable persons belonging to this profession. Another weakness of the pedigree method is that it affords no check on the actual parentage of offspring. The mother is usually not in doubt, but there is often some question as to the actual father. This is principally true in connection with the study of pedigrees of feeble minded and delinquent stocks and of primitive peoples with moral codes somewhat less rigid than our own. In other words, the genetic data acquired by this method are not scientifically controlled. Still another weakness of this method is that it is not always possible to distinguish between conditions that are hereditary and those due to disease or poor environment. In spite of these weaknesses, the pedigree method has brought to light a great deal of valuable information about human heredity. So long as one retains a properly critical attitude toward data and conclusions, no harm and much good may accrue from a reveiw of the principal results of this method of research.

Two postulates underlying the study of the heredity of human traits may be set down as follows: (1) When characters are inherited according to the laws of Mendel, that is, when one of a pair of characters is dominant, or partly so, and the other recessive, and they segre-

gate in Mendelian ratios in subsequent generations, such character differences are determined by genes (2) Allelomorphic differences have arisen through the process of gene mutation, a process so well established for lower organisms These postulates are justified, for it is hardly likely that so universal a method of heredity as the Mendelian method operates for the rest of the organic world and not for man Also, the method of gene mutation is the only method by means of which allelomorphic differences are yet known to arise, and it is hardly likely that man is an exception to the rule

The rate of mutation for man has been worked out for various races of mankind The number is almost the same in the various races For every 115 normal genes in the Russian race there are about 5 more mutant genes than in the Negro race "If 6 000 generations ' says Danforth, "represents anywhere nearly the time since these two groups along with others, diverged from a common ancestor, these additional mutant genes must have been acquired in this length of time These figures indicate that in the course of 6 000 generations at least 5 in every 115 gene lines which have persisted underwent mutation in this one direction Since there is no evidence of selection, this may be presumed to be the rate of mutation in this particular germplasm, from which it follows that there has been on the average, one mutation in every generation for each 138 000 genes If, as some might be inclined to think the two germplasms have passed through more than 6 000 generations since they separated the rate of mutation has been less than this "

Thus we see that mutations, though infrequent, continue to appear at a slow and steady rate Like the mutations in *Drosophila* and those of other animals studied the majority of mutations in man are poor, many are indifferent, and very few are good It has evidently taken a long time for man to acquire the better hereditary traits he now possesses In the past, natural selection has tended to eliminate most of the undesirable mutants, especially the dominant ones, but under civilized conditions mankind has done much to nullify the good work of natural selection by doing everything in his power to preserve the poorer mutants and help them to multiply

SOME HEREDITARY TRAITS IN MAN

Studies of nearly 200 human traits have been made In the majority of cases they can be classified as dominants, ordinary recessives, and sex linked recessives The latter are the easiest to detect, for

they follow the familiar mode of heredity described for sex linked characters in *Drosophila* Dominants may fairly readily be distinguished by the fact that at least one of the parents, one grandparent, one great grandparent, etc. exhibit the character, a dominant character appears in every generation Ordinary autosomic, or non sex linked, recessives are characterized by the irregularity of their incidence in pedigrees They may skip one or several generations and *only appear at all when the same recessive gene is present in the germ* plasm of two mating individuals in which case it will appear in the following ratios according to the genetic make-up of the parents (*a*) *If both are heterozygous three out of four offspring will show the dominant* and one the recessive character, (*b*) if one is a heterozygote and one a recessive the offspring will be half heterozygous dominants and half recessives Thus we see that recessive characters may be hidden for a long time awaiting a favorable mating to give them expression

Most of the best pedigrees of human characters deal with relatively rare and atypical or abnormal characters, in fact, most of them deal with what we ordinarily call freaks or pathological conditions The reason for this is that rare and unusual conditions are much more easily detected and recognized Ordinary, common differences are hard to detect and hard to distinguish, and therefore difficult to follow in pedigrees

It is not our intention in this chapter to attempt an exhaustive treatment of the facts of heredity ascertained by the pedigree method We shall merely list some of the commonest cases of hereditary characters and give a few pedigrees illustrating them

The *following is a list of human unit characters classed as dominants*, ordinary recessives and sex linked recessives

A DOMINANT CHARACTERS

Skin and Hair	
Dark skin	Dominant over blond or albino (probably due to two or more pairs of genes)
Spotted with white	Dominant over uniformly colored
Tylosis and ichthyosis	Thickened or scaly skin
Epidermolysis	Excessive blisters of skin
Brown or black hair	Dominant over red and flaxen (probably due to more than one gene)
Red hair	Dominant over flaxen
Beaded hair	Single hairs are not uniform in diameter

White forelock	White patch of hair in front
Hypotrychosis	Hairlessness associated with lack of teeth
Pattern baldness	Partly sex limited
Eyes	
Front of iris pigmented (eyes black brown hazel etc.)	Dominant over lack of pigment in front of iris (blue eyes)
Hereditary cataract	Opacity of lens
Night blindness when not sex linked	Inability to see in dim light
Displaced lens	Causing defective vision
Glaucoma	Swelling of eyeball due to internal pressure
Coloboma	Open suture of the iris
Pigmentary degeneration of retina	Causing blindness
Skeleton and Muscles	
Brachydactyly	Digits lacking one joint
Polydactyly	Extra digits
Syndactyly	Fused or webbed digits
Symphalangy	Fused joints of digits stiff fingers
Split hand	Palm cleft to the wrist
Lobster claw	No digits but thumb
Exostoses	Abnormal outgrowths of long bones
Brittle bones	Bones very fragile
Absence of palmaris longus muscle	Lack of a certain muscle in palm of hand
Muscular atrophy	Partially dominant
Body Build	
Achondroplasy	Dwarfs with short, stout limbs normal body and head
Short stature	Partly dominant over tallness
Obesity not due to glandular defects	Partially dominant
Nervous System and Kidneys	
Huntington s chorea	A type of St Vitus dance
Diabetes insipidus	Partially dominant
Diabetes mellitus	Partially dominant

B AUTOSOMIC RESESSIVE CHARACTERS

Albinism	Lack in pigment in skin and hair—sometimes pink eyes
Ateleosis	True dwarfs body small with parts in normal proportions
Cretinism	Dwarfism due to hereditary thyroid deficiency

Alkaptonuria	Urine dark after oxidation
Otoschlerosis	Thickening of ear-drum
Left handedness	Probably recessive
Tendency to twinning	Probably recessive
Susceptibility to tuberculosis	Probably recessive
Thomsen's disease	Lack of muscular tone
Menier's disease	Dizziness and roaring in ears
Deaf mutism	Congenital deafness
Friedereick's disease	Degeneration of the upper part of the spinal cord
Multiple schlerosis	Diffuse degeneration of nervous tissue
Chorea	Ordinary St Vitus dance
Hereditary feeble mindedness	Probably recessive
Hereditary epilepsy	Probably recessive
Manic depressive insanity	Probably recessive
Dementia praecox	Probably recessive

C CHARACTERS DUE TO CUMULATIVE FACTORS

It is suspected that a good many of the characters listed as incompletely dominant may be due to cumulative factors producing the condition usually called blending heredity Those that almost certainly belong to this category are stature body weight (except certain types of obesity) skin color, shape of head and proportions of features

D SEX LINKED RECESSIVES

Color blindness	Lack of discrimination between red and green
Night blindness	One form of this defect which involves inability to see in dim light
Haemophilia	Free bleeding
Gower's disease	Muscular atrophy
Neuritis optica	Progressive atrophy of the optic nerve

Some pedigrees of dominant characters —Perhaps the best example of a dominant trait that has been thoroughly worked out is *brachydactyly*, a type of hand in which one joint is lacking in each digit In the normal hand the thumb has one less joint than the fingers Hence in a brachydactylous person all the fingers are thumbs and the thumb is a subthumb Such a type of hand is broad thick, and clumsy It is not at all a well adapted character, but it is not so bad but that it can survive Drinkwater has studied a number of brachydactylous pedigrees one of which is shown in Figure 81 Males in this chart are shown by ♂ and females by ♀, solid circles indicate affected

and open circles unaffected individuals Notice that the character appears in at least one parent in each generation, which is characteris

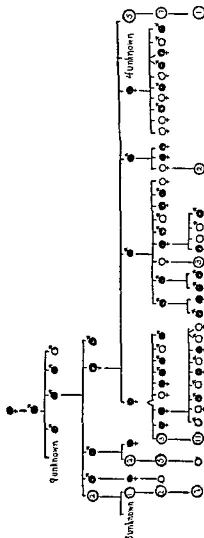


FIG 81 — Pedigree of a line with brachydactyly, condensed and modified from Drinkwater's chart It reads thus A brachydactylous woman has a son, also brachydactylous He has thirteen children, the condition of nine of whom is unknown, three possess the character, one is normal One of these four known sons, himself brachydactylous, has six children The sex of two is not known, but they were not brachydactylous, three sons and one daughter were And so the family continues One sees at a glance how the defect continues generation after generation, not reappearing, however, in the offspring of those who are free from it (*From Downing*)

tic of the mode of inheritance of dominant characters Also the number of individuals affected is about what one would expect in the case of a dominant character

The question arises with reference to this, as well as to many other, dominant characters as to why, being dominant, the character does not become more prevalent rather than remaining relatively rare The answer that seems most probable is that the brachydactylous hand is very poorly adapted to human uses and those individuals possessing it are seriously handicapped Hence there may be marriage selection against it If it were more advantageous than the normal, doubtless the incidence of the character would increase and it might in time become the typical condition for the species The same explanation would apply equally well to all other cases of dominant abnormal

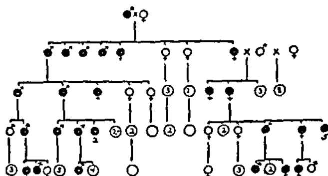


Fig 82 — Inheritance of one form of cataract Modified from Nettleship's chart The diagram reads thus A man with cataract married a normal woman of their eight children six were affected with the disease One of these married an unaffected man three of the children of this union were normal sex unrecorded, two defective This same man married a second wife who was normal, their eight children were all unaffected So continue reading through five generations (*From Downing*)

Mendelian traits It might also be asked why all the offspring of a dominant parent do not show the character The reason should be obvious, namely, that most individuals are heterozygous for the character A heterozygote mating with a recessive is expected to produce one half heterozygotes and one half recessives, which is about what the accompanying pedigree shows

Another case of a dominant character not so definitely analyzed as the last is a type of *hereditary cataract* (Fig 82) This condition is due to an opaque region in the lens of the eye, which, when well advanced, may cause blindness "In the particular form of the disease here considered," says Downing, "it does not develop until middle life

Clarence Loeb in a study of hereditary blindness tabulated the results of 304 families in which such blindness occurs There were 1,012 children, of whom 58 per cent were afflicted, which is about the percentage expected when hybrid defectives mate with normal individuals and the defect is a dominant character "

A typical pedigree of a recessive character.—A good example of the mode of inheritance of an uncommon recessive character is shown in Figure 83, the pedigree of a family line showing outcropping of *albinism*, lack of pigment in hair, skin, and eyes It is noteworthy that the appearance of the character is relatively rare, only 19 out of 158 individuals in the pedigree being albinos or partial albinos, that albino offspring are produced by two phenotypically normal (pigmented) parents, and that in generation VII, where several of the children are albinos the two parents are descended from common ancestors a few generations back, and are undoubtedly both heterozygous In this pedigree there are no cases of the mating of two albinos If such matings had occurred, the expectation, of course, would be that all offspring would be albinos Since we shall have to present further examples of pedigrees of recessive characters in connection with the account of the heredity of mental characters, we need give no further examples here

It is also unnecessary to repeat in this place the description of such sex linked human characters as color blindness, haemophilia, etc The accompanying chart (Fig 84), which represents an investigation of a Texas family connection made by the writer in 1910, is typical for sex linked characters The existence of sex linked heredity in man goes far to support the contention of eugenists that heredity in man follows the same rules as have been found to hold for the lower animals

As an example of human characters probably determined by *cumulative factors*, we may cite the case of skin color Whole races of man are dark skinned, others light skinned Some idea as to the mode of heredity of skin color is obtained by studies of crosses between negro and white individuals "In a cross between a negro and a white person," says Castle, "children are produced that are of an intermediate, but frequently variable skin color, and are known as mulattoes Mulattoes mating inter se produce an F_2 generation of highly variable skin color but rarely pure white Davenport has concluded that two independent Mendelian factors affecting skin color are involved This explanation would lead us to expect one in sixteen of the F_2 mulatto offspring to have skin as white as an European, even though his negro

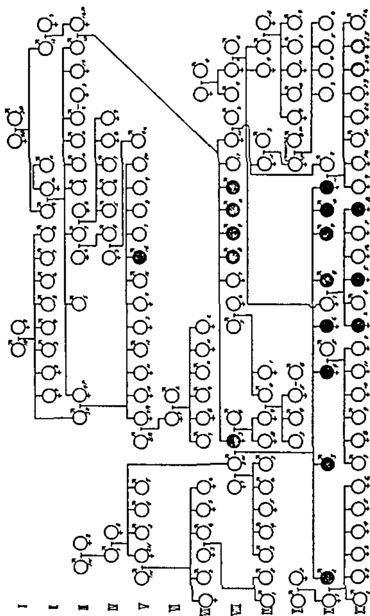


FIG 83 — Pedigree showing heredity of albinism (black symbols), shaded symbols indicate partial albinos (*From Davenport, in Castle et al, Heredity and Eugenics*)

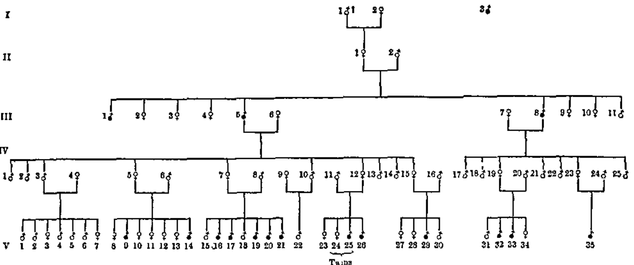


Fig 84 —A pedigree of five generations of a family showing sex linked night blindness (inability to see in dim light) Black symbols indicate those affected Note that all those affected are males (*From Newman*)

ancestry might show in other characteristics such as curly hair, broad nose thick lips etc It is difficult to get any wholly satisfactory evidence either for or against this explanation That published by Davenport can scarcely be considered conclusive for the data studied are derived from a population in which illegitimacy by Davenport's own statement is as high as 72 per cent On the whole, it seems probable that segregation of skin pigmentation in mulattoes is either incomplete or rarely complete because multiple or modifying factors are involved"

Having given examples of pedigrees of physical characters exhibiting all of the principal modes of Mendelian heredity let us now pass to a consideration of the facts about the heredity of mental traits in man as revealed by pedigree studies

HEREDITY OF MENTAL TRAITS IN MAN

The studies of the heredity of mental traits in man consist principally of those of exceptional genius and of definite mental defects and abnormalities Very little effort has been expended upon the heredity of normal average intelligence such as the great majority of us possess

Long ago in 1869 Sir Francis Galton published a fascinating book on *The Heredity of Genius* in which he presented a large number of pedigrees of families showing definite and special types of genius, such as musical genius genius for astronomy and mathematics, genius for science etc Among those described in some detail are the Bach family of great musicians in Germany the Herschell family of great astronomers in England and he might have added his own pedigree composed of the interrelated families of Darwins Galtons, and Wedgewoods the present generation of which consists of many outstanding and influential persons (Fig 85) No family today shows more plainly than this one what can be done in the way of racial improvement through a certain amount of concentration of good germ plasm by judicious inbreeding (cousin marriages) when the inbreeding stocks are strong and sound Charles Darwin the most eminent member of this family connection was the son of an eminent physician a member of the Royal Society One of Darwin's grandfathers was the well known Erasmus Darwin referred to in the *History of Evolution* (chap ii) The other grandfather was Josiah Wedgewood F R S, founder of the Wedgewood potteries Charles Darwin married his own cousin Emma Wedgewood Four of Darwin's sons are eminent members of

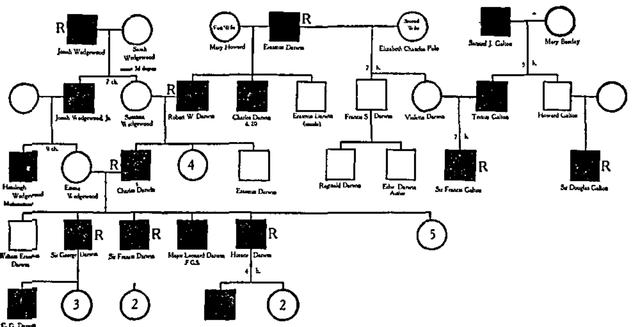


FIG 85 —Pedigree of the Darwin Galton Wedgewood Family Males of note black squares an *R* beside square denotes membership in the Royal Society Figures in circles show number of daughters if more than one

the Royal Society, one of them being Major Leonard Darwin, president of the Second International Congress of Eugenics, from whose speech we quoted a paragraph in the previous chapter Darwin's aunt married into the famous Galton family and her son was the late Sir Francis Galton, the originator of the term "eugenics," whose work we have just referred to This is perhaps the greatest eugenic family on record

The Bach family of musicians is another outstanding example of the heredity of genius The best known member of the family is the famous Johann Sebastian Bach In six generations of Bachs there were 47 musicians of note, 29 of whom ranked high in musical circles Johann Sebastian Bach was married twice and both times to a relative bearing the name of Bach His father married an aunt. There was a great deal of rather close intermarriage in the family, which seems to have helped to concentrate and preserve the high qualities of the stock

Most of the work done on the heredity of mental traits has been expended on the study of *defective and abnormal heredity, including* feeble mindedness and the various so-called ' insanities "

The heredity of Feeble-mindedness —Feeble mindedness, as defined by Goddard is "a state of mental defect existing from birth or from an early age and due to incomplete or abnormal development, in consequence of which the person affected is incapable of performing his duties as a member of society in the position of life to which he is born ' This is not a very exact definition, for, according to the statement, a normal individual born into a community of geniuses might be classed as feeble minded More specific are the following definitions *of various types of mental defectives* An *idiot* is one who, *when adult,* has no greater capacity to learn than a child of two years or less An imbecile is one who rates mentally between two and seven years A moron is one who rates mentally from seven to twelve years Usually the so called feeble minded ' individual is either an imbecile or a moron and much more often the latter than the former Obviously, then, there are many kinds and degrees of feeble mindedness, and it will often be difficult to draw the line between the high grade moron types and the lower levels of normal individuals ' This classification says East, is arbitrary, but it serves a useful purpose when dealing with feeble mindedness as a social problem Medically and genetically it means nothing—at present If this is true, and we believe it at least largely so attempts to deal with feeble mindedness as a simple Mendelian recessive are likely to be only partially successful

We must, therefore, take all genetic studies of feeble mindedness with a grain of salt

H H Goddard, probably the most distinguished of the students of feeble-mindedness, has studied many pedigrees and compiled statistics concerning 300 of the best of these Of the cases of feeble mindedness diagnosed as such by him, 164 (54 per cent) are considered unquestionably hereditary, 71 (23 per cent) probably hereditary, and the rest probably non hereditary Goddard seems to be convinced that feeble-mindedness is due to a single recessive gene He cites 42 cases in which heterozygous, phenotypically normal mothers (NF), when mated with feeble-minded fathers (FF) produced 71 feeble-minded and 73 normal offspring out of a total of 144 This is almost too close an approximation to the expected Mendelian ratio of 1 to 1 From 26 matings of apparently heterozygous fathers and mothers (presumably NF) there were produced 122 known children, 83 of whom were normal and 39 feeble minded suggesting the expected Mendelian ratio of 3 to 1 Of 476 children of parents both of whom were feeble minded (FF), only 6 were normal in intelligence, and these are suspected of being illegitimate In Figures 86 and 87 are presented two typical pedigrees of feeble-minded families studied by Goddard The first of these pedigrees (Fig 86) shows the dire effects resulting from the interbreeding of feeble-minded parents The children are all feeble-minded except the considerable number that died in infancy, presumably because of neglect and ignorance of the parents The second pedigree (Fig 87) illustrates what approximates a controlled scientific experiment, for one woman was married twice, once to a normal man and once to a feeble minded man, and had several children by each All of the offspring from the normal father are normal (but evidently heterozygotes), while all those of the feeble-minded father were feeble minded and otherwise abnormal

It is interesting to note that a very large proportion of juvenile criminals and prostitutes when given the Binet test, rank as feeble-minded Tests of juvenile criminals in various states show the following facts In New Jersey 46 per cent of juvenile criminals are feeble minded, in Ohio, 70 per cent, in Virginia, 79 per cent, and in Illinois, 89 per cent It would seem to be a conservative estimate that fully half of juvenile criminals are feeble minded

It has also been shown that the great majority of prostitutes and girls who have been placed in reformatories for sex delinquency are feeble minded Tests of large numbers of girls in an Illinois reforma

tory show that 97 per cent are feeble-minded. In Massachusetts a prominent commission reports that of 300 immoral women under detention in that state 57 per cent were feeble-minded, while the rest rated from nine to twelve years in mental age. On the basis of data

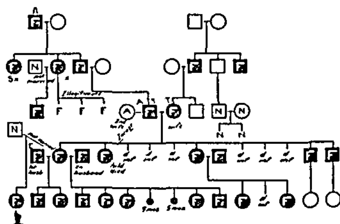


Fig. 86.—Pedigree of a family with a high proportion of feeble-minded persons (*F*). Squares, males; circles, females; *d. inf.*, died in infancy. (*From Davenport after Goddard.*)

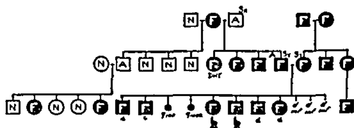


Fig. 87.—Pedigree of a family in which the feeble-minded grandmother married twice: by a normal husband she had normal children, but by an alcoholic sex-offending (*Sx*) doubtless feeble-minded husband she had only feeble-minded children. (*From Davenport after Goddard.*)

such as these Goddard and others maintain that there is a very intimate relation between crime, vice, and feeble-mindedness. "Wipe out the feeble-mindedness," say they, "and you wipe out most of the vice and crime."

Feeble-mindedness has come to be the most pressing of all eugenic problems—one that should at once be recognized and solved if possible

Statistics seem to indicate that this defect is on the increase, certainly it is far too common to be ignored Records show 178,000 mental defectives in Great Britain and Ireland in 1921, and these include only the very positive cases It has been estimated by one expert that in the United States one person in every 294 is feeble-minded, by another expert, one in every 138 In Indiana it is claimed that over 2 per cent of the population of ten unselected counties are mental defectives If the incidence is the same in the whole state, there are 56,000 defectives in Indiana alone, and Indiana is in no way exceptional Calculations indicate that in the United States as a whole there are not less than half a million feeble minded individuals, and several times that many individuals phenotypically normal but carrying the gene or genes for feeble mindedness A large proportion of these individuals are charges of the various states and cost the public many millions of dollars annually without contributing anything of value to the community

Insanity and heredity —A great deal of careful work has been done on the heredity of insanity For example, *David Heron* in Scotland has studied 331 family histories exhibiting insanity There are several distinct and different conditions included under the blanket term "insanity" It is obvious that they could not all be determined by the same gene or genes Heron's data on insanity are summed up in the following table

HERON'S DATA ON THE HEREDITY OF INSANITY

Parents	Offspring		
	Insane	Sane	Percentage of Insane
Both sane	314	1179	21
One insane	93	299	24
Both insane	4	4	50

These figures are not at all readily fitted into any simple Mendelian ratio Doubtless the various insanities are not due to single Mendelian units, but are complex cases That they are to some extent and in some manner hereditary, seems beyond question

Rosanoff and Orr, two prominent American psychiatrists, seem somewhat more sanguine about fitting the insanities into the Mendelian system Their data are given here in tabular form

ROSANOFF AND ORR (DATA ON INHERITANCE OF INSANITY)

(N = Normal I = Insane)

Parents	Matings	Children		
		Neuropathic	Normal	Mendelian Expectancy
Both insane (II)	17	54	10*	All insane
Only one insane (NI×II)	93	190	239	1 : 1
Only one insane (NN×II)	14		45	All insane
Both normal (NI×NI)	62	107	215	1 : 3
Both normal, one heterozygous (NN×NI)	20		77	All sane

* Eight have not passed the age of incidence.

These data might readily be taken to prove that insanity is a simple Mendelian recessive, but a scrutiny of the methods of collecting data make geneticists somewhat skeptical. "The data," says Castle, "have the scientific value of gossip, consisting of answers made by informants to leading questions designed to bring out any weakness in the pedigree. Like inquiries made concerning any individual in the community would show him an unmistakable victim of insanity. Three fourths of their persons insane for pedigree purposes would be classed as fully normal if they occurred in families free from insane patients. Such classification has little scientific value." This statement may be severe, but it seems justified by the fact that persons who are described as "a crank," "easily excited, nervous temperament," "very nervous," "erratic, excitable," "nervous, little things bothered her, worried a great deal," are classed as insane. Doubtless many of us who think we are normal might be classed in some of these categories by our acquaintances.

As yet it would be quite unsafe to classify any of the insanities as simple Mendelian unit characters. The subject is a very complex and difficult one, and genetic results will continue to be unsatisfactory until the psychiatrists are able more accurately to diagnose and classify the insanities.

Pedigrees of royal families.—Members of royal families have been used as data for the study of human heredity. Records of these individuals and their traits are preserved in the archives and should furnish good material for genetic study. The well known writer Frederick Adams Woods has made an exhaustive study of the pedigrees of European royal families and has published the results of these studies

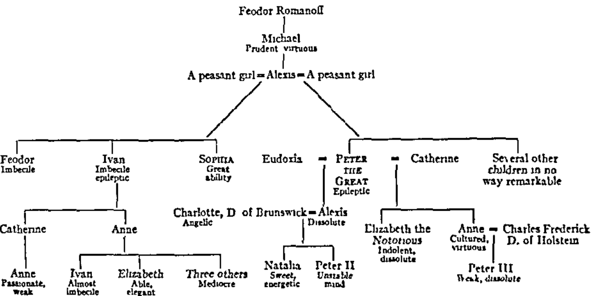
It happens that rather complete data about the members of royal families are to be found in biographical dictionaries From these sources it is usually possible to form a fairly accurate estimate of the capacities of these persons In addition the portraits of most members of royal families are preserved in art galleries The following summary of F A Woods' findings is quoted from Professor E R Downing

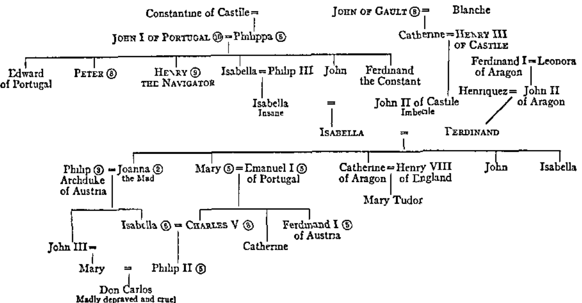
"Early modern European history centers about the doings of a few great men and women Peter the Great of Russia, Ferdinand and Isabella and Charles V of Spain, Frederick the Great of Prussia, Gustavus Adolphus and Charles XII of Sweden, are among the most brilliant of these potent individuals that shaped the destinies of Europe during this period It is interesting to note how their characters are determined (and through them national destinies are apparently decided in no small measure) by the hereditary concentration of ability due to lucky royal matings and how their genius is dissipated by unwise matings

"Peter the Great of Russia came as a brilliant type from a good stock though with a very evident taint of epilepsy and feeble mindedness He himself was an epileptic His father, grandfather, and great grandfather had been men of large ability They had married peasant girls, as was the custom of the czars Peter s own brothers and sisters were in no way remarkable His half sister Sophia was a woman of marked ability, although two of her brothers were imbeciles one also an epileptic As will be seen from the pedigree the epilepsy imbecility, and mediocrity appear in both Peter s children and grand children, as well as in those of his imbecile half brother, Ivan It is interesting to note from the pedigree that the feeble mindedness and epilepsy seem to cling to the males quite persistently The females of the family are much more apt to be brilliant and virtuous Peter the Great's own son Alexis was a poor dissolute specimen, and although he married Charlotte, the angelic daughter of a great line the house of Brunswick, the son of this mating was Peter II, of unstable mind, while the daughter Natalia was as sweet as she was energetic

'Isabella and Ferdinand were both descendants from lines of very great individuals, although in each case there is insanity in the family Isabella herself comes from an insane mother and an imbecile father, but her grandparents and great grandparents were well balanced and able The data for the charts of these royal families were taken largely from F A Woods's *Mental and Moral Heredity in Royalty* supplemented with information from other sources He grades the

THE ROMANOFFS OF RUSSIA PETER THE GREAT



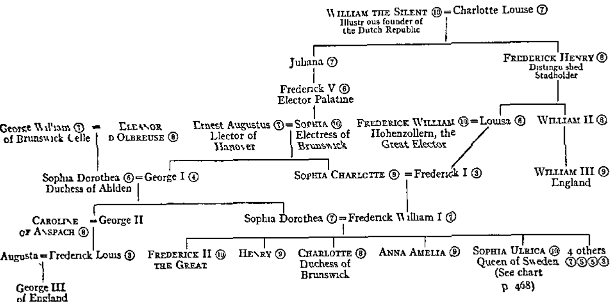

FERDINAND AND ISABELLA
Constantine of Castile =
JOHN I OF PORTUGAL (10) = Philippa (6)
JOHN OF GAULT (8) =
Blanche
Catherine = HENRY III OF CASTILE
Ferdinand I = Leonora of Aragon
Edward of Portugal
PETER (8)
HENRY (9) THE NAVIGATOR
Isabella = Philip III
John
Ferdinand the Constant
Henriquez = John II of Aragon
Isabella Insane
=
John II of Castile Imbecile
ISABELLA
=
FERDINAND
Philip (3) Archduke of Austria = Joanna (2) the Mad
Mary (5) = Emanuel I (5) of Portugal
Catherine of Aragon = Henry VIII of England
John
Isabella
Mary Tudor
Isabella (6) = CHARLES V (8)
Catherine
Ferdinand I (5) of Austria
John III =
Mary
=
Philip II (6)
Don Carlos
Madly depraved and cruel

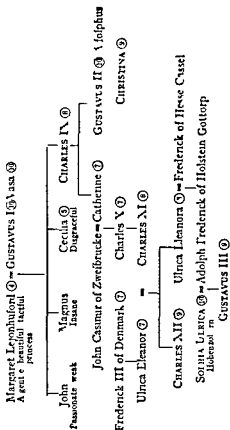
individuals on a scale of 10 Ten represents very high ability, as determined by the comparative amount of space and laudation given to the individual in such standard works as Lippincott's *Biographical Dictionary* Five out of eight of Isabella s great grandparents rank very high John the Great of Portugal, twice her great grandfather, has a grade of 10 John of Gault twice her great grandfather, has a grade of 8, as does also John of Castile, while Henry III of Castile, one of her grandparents, is designated the model king Ferdinand I of Aragon, the grandfather of Ferdinand, is a brother of this same Henry III of Castile and is also an exceedingly able king Of the children of Ferdinand and Isabella, most were mediocre or distinctly inferior Joanna was insane In the next generation, however, appears Charles V whose reign marked the acme of Spain s greatness, partially due to his own ability, partially due to the momentum of those movements that were instituted by his illustrious grandparents Charles V married his own cousin, as did also John III Children of these two matings married, and Don Carlos child of this latter marriage, was madly depraved and cruel

"When insanity and brilliancy are found in the ancestry it seems merely a matter of chance as to whether the determiners for greatness will be thrown together in the union of sperm and egg or those for insanity We can predict with some certainty,that, in a large number of offspring ability will reappear and insanity will reappear, but just what individual each will strike it is impossible to prophesy without knowing much more definitely the nature of the germ plasm involved One may say that the convergence of a number of lines of descent from great ancestors toward one individual makes it probable that he will be exceptionally able

"This is nowhere better illustrated than in the family tree of Frederick the Great of the Prussian house of Hohenzollern, as will be seen from the chart on page 467 Of his great grandparents, three scale 10, one 9, one 8, two 7, and one 6 Not one is below mediocrity, and the majority are of very high grade Of his fourteen ancestors back three generations, only one is distinctly inferior Of his brothers and sisters four are distinctly great, three mediocre, and one inferior

"It is interesting to trace the effect of the mating of such splendid stock with another brilliant line that of the Swedish royal house Gustavus I, or Gustavus Vasa, is another instance of the brilliant mutant, with some taint of neurosis He married a gentle and tactful princess their son Charles IX was a very able man, although of their


THE HOHENZOLLERNS OF PRUSSIA PEDIGREE OF FREDERICK THE GREAT
William the Silent ⑩ = Charlotte Louise ⑦
Illustrious founder of the Dutch Republic
Juliana ⑦
Frederick Henry ⑧ Distinguished Stadholder
Frederick V ⑥ Elector Palatine
George William ⑦ of Brunswick Celle
Eleanor d'Olbreuse ⑧
Ernest Augustus ⑦ Elector of Hanover
Sophia ⑩ Electress of Brunswick
Frederick William ⑩ Hohenzollern, the Great Elector
Louisa ⑥
William II ⑧
Sophia Dorothea ⑥ = George I ④
Duchess of Ahlden
Sophia Charlotte ⑧ = Frederick I ⑨
William III ⑨ England
Caroline of Anspach ⑧
George II
Sophia Dorothea ⑦ = Frederick William I ⑦
Augusta = Frederick Louis ③
Frederick II ⑪ the Great
Henry ⑨
Charlotte ⑧ Duchess of Brunswick
Anna Amelia ⑨
Sophia Ulrica ⑩ Queen of Sweden (See chart p 468)
4 others ⑦⑤⑤③
George III of England


CHARLES THE GREAT (XII) OF SWEDEN
Margaret Lejonhuford (4) = GUSTAVUS I (10) Vasa (10)
A gentle beautiful tactful princess
John
Passionate weak
Magnus
Insane
Cecilia (5)
Disgraceful
CHARLES IX (8)
John Casimir of Zweibrucke = Catherine (7)
GUSTAVUS II (10) Adolphus
Frederick III of Denmark (7)
Charles X (7)
CHRISTINA (9)
Ulrica Eleanor (7) = CHARLES XI (6)
CHARLES XII (9)
Ulrica Eleanora (5) = Frederick of Hesse Cassel
SOPHIA ULRICA (10) = Adolph Frederick of Holstein Gottorp
Hohenzollern
GUSTAVUS III (9)

three other children one was insane and two weak The children of Charles IX were both remarkably able The daughter Catherine becomes the mother of a later succession of kings Her son Charles X and his son Charles XI were rather mediocre but Charles XI with this fine stock behind him, married Ulrica Eleanor (7), granddaughter of Christian IV of Denmark, the most brilliant of all Danish sovereigns, and Charles XII, their son, is pronounced by Voltaire the most remarkable man who ever existed Charles XII had no children the succession passed to his sister's son, Adolph Frederick of Holstein-Gottorp, who married Louisa Ulrica, sister of Frederick the Great of Prussia The result of this union of two great lines of hereditary ability was Gustavus III, a fit successor of Gustavus Vasa, Gustavus Adolphus, and Charles XII, he was 'a prodigy of talents,' statesman poet, dramatist."

CHAPTER XXXVI

THE STATISTICAL STUDY OF HEREDITY IN MAN

Introduction —A good example of this method is afforded by Popenoe and Johnson's studies of the heredity of longevity (chap xxxix) Other examples are found in Heron's and in Orr and Rosenoff's studies of the heredity of insanity presented in the last chapter The proof of a given character being hereditary is believed to be attained when it is shown that affected parents have a significantly larger proportion of affected offspring than have non affected parents

The statement that twinning is hereditary is based on the fact that twins are far more common in certain strains than in the general population A twin birth occurs in about 1 out of every 88 confinements C H Danforth found that in the case of 50 newborn twins there were 171 single brothers and sisters and 10 pairs of twin brothers and sisters, a ratio of about 1 to 18, as compared with that in the general population, 1 to 88 Moreover, with respect to the mothers of these twins, their brothers and sisters numbered 318 singles to 10 pairs of twins, a ratio of 1 to 32 With respect to the fathers of these twins, there were 219 brothers and sisters born singly and 8 pairs of twin brothers and sisters a ratio of 1 to 37 A number of similar studies give comparable results showing that twinning has a hereditary basis, but indicating nothing as to the exact mode of heredity

The strength of heredity between different groups of relatives has been determined for a large number of human characters by determining the coefficient of correlation (see chap xliii) existing between selected groups Complete correlation is represented by the unit, 1 If correlation is 1, heredity is perfect, and various grades of imperfect heredity are represented by decimals, such as 0 9 0 6, 0 25 etc It has been shown that for most characters the correlation of offspring to fathers is about 0 4, the same to mothers The correlation between sibs (brothers and sisters) is about 0 5, that between cousins about 0 25, that between one-egg (identical) twins 0 9+ These indices of correlation run strictly parallel with degrees of closeness of genetic relationship

GALTON S STATISTICAL STUDIES OF HEREDITY IN MAN

Galton was the first to make extensive use of the statistical method of studying the degree of heredity existing between parents and off spring and between sibs

H s first investigation concerned itself with the heredity of stature a highly variable character in man He tried to find just how nearly parents and offspring are correlated as to adult stature Certain dif ficulties were met at the outset First there is a pronounced sexual dimorphism in stature males being considerably taller on the average than females To get rid of this difficulty he first determined that males are on the average about 1 inch to the foot taller than females and then transmuted all female statures into equivalent male statures by adding an inch to the foot to the stature of each female Second there are always two parents and they may be of very different stat ures even after the mother s stature is transmuted into the male equivalent To overcome this difficulty he averaged the statures of each pair of parents and called it the mid parent stature The stat ures of the mid parents were grouped into nine classes ranging from 64 to 73 inches each class having a range of an inch Thus one class consisted of those mid parents falling between 72 and 73 inches the next class from 71 to 72 inches and so on down to the shortest class from 64 to 65 inches The following schematic diagram (Fig 88) shows the extent to which offspring inherit stature differences from the parents If heredity were perfect parent and offspring statures would coincide on the diagonal l ne but they do not coincide Average parents have nearly average offspring but very tall and very short parents have offspring decidedly less tall or less short respectively than their parents In the chart the arrow heads indicate the points where the average statures of offspring of each of the mid parent classes fall Note that mid parents which average a little over 64 inches have offspring averaging about $65\frac{1}{2}$ inches and that mid parents which have an average stature of $71\frac{1}{2}$ inches have offspring averaging 70 inches It is clear that on the average the more exceptional the mid parents are the more the offspring regress toward the mean stature of the group or toward mediocrity This is true of all but the extreme tall group where there is only a half inch of regression in the offspring The reason for this is probably associated with the fact that very tall persons are homozygous (double recessives) shortness of stature being incompletely dominant over tallness

Galton calculated that with regard to stature the offspring of

exceptional parents tend to be on the average, one third less exception al than the parents This he called the *Law of Filial Regression*

Similar results were obtained with several other types of human differences that were capable of being graded quantitatively and arranged in classes Thus when eye colors were graded on the basis

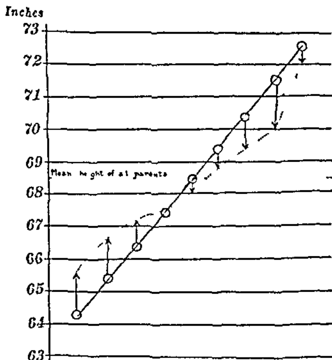


Fig 88—Diagram to illustrate Galton s Law of Filial Regression as shown in the stature of parents and children The mean height of all parents is shown by the dotted line between 68 and 69 inches The circles through which the diagonal line runs represent the heights of graded groups of parents and the arrow heads indicate the average heights of their children The offspring of undersized parents are taller and of oversized parents are shorter than their respective parents (*From Conklin after Walter*)

of the amount of pigment in the iris and arranged in nine or ten classes it was found that there was practically the same amount of filial regression as there was in the case of stature This was true for all except the pure blue eyed parents, with no pigment in the front of the iris where no regression in the offspring was noted Blue-eyed individuals are of course, homozygous, if they are really blue-eyed in the genetic sense

The same law was shown to hold also for mental characters, or grades of mental ability "The more bountifully a parent is gifted by nature," says Galton, "the more rare will be his good fortune if he begets a son as richly endowed as himself" Galton considered that any law that applied to such diverse characters as stature, eye color, and mental ability must be a universal law of heredity

The problem then arose as to the reason why heredity between parents and offspring is so imperfect Let us remember that Galton did all his work long before the rediscovery of Mendel's publications Had he known about Mendel's laws, about the difference between

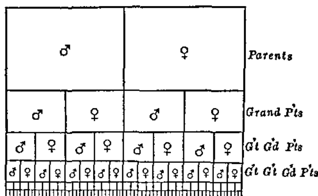


FIG 89—Diagram to illustrate Galton's "Law of Ancestral Shares in Inheritance" The whole heritage is represented by the entire rectangle that derived from each progenitor by the smaller squares, the number of the latter doubles in each ascending generation while its area is halved. (*From Conklin, after Thomson*)

phenotypic and genotypic conditions, and that recessive characters concealed for some generations crop out when two recessive genes meet, he would have understood at once why offspring are not always as exceptional as parents Without any of this background, Galton had to solve the problem of imperfect heredity in his own way

He arrived at a conclusion not unlike that of Weismann, that inheritance does not come from the bodies of parents but from a racial "stirp," which is about the same as Weismann's "germ plasm" The reason assigned for filial regression was that offspring do not get all their hereditary characters from their immediate parents, but some of it comes from the four grandparents, some from the eight great grandparents, and some from more remote ancestors Just how much each of the different grades of ancestors contribute to the total heritage of

an individual was worked out by statistical methods, and the result was Galton's *Law of Ancestral Shares in Inheritance* (Fig 89)

According to this law, the two parents contribute between them on the average about one half of each inherited character, each parent contributing a quarter of the whole The four grandparents combined contribute one-half of the remainder or one-fourth of the whole, each of them one sixteenth The eight great grandparents contribute half of the remaining one quarter or one-eighth of the whole, each contributing one sixty fourth The remaining ancestors contribute the remaining eighth The total heritage would be 1 This is an infinite mathematical series whose principal property is that each term is *equal to the sum of all those which follow* thus $\frac{1}{2} = \frac{1}{4} + \frac{1}{8} + \frac{1}{16} + \frac{1}{32} + \frac{1}{64}$, etc No account is taken of the prepotencies of particular ancestors—and there is no question that such prepotencies exist—but all individual peculiarities are averaged up The results are mass results, inapplicable to any particular individual or pedigree

The exact shares of various grades of ancestors, as stated by Galton, have been questioned by Pearson who, after careful study, has revised Galton s figures to read parents $\frac{1}{3}$, grandparents $\frac{2}{9}$, great grandparents $\frac{4}{27}$ etc

Criticism of Galton's work.—The scheme used by Galton assumes that the number of ancestors is far greater than is actually the case "Theoretically," says Conklin, "the number of ancestors doubles with each ascending generation, there are two parents, four grandparents eight great grandparents, etc If this continued to be true indefinitely the number of ancestors in any ascending generation would be $(2)^n$, in which n represents the number of generations There have been 57 generations since the beginning of the Christian Era and if this rule held true indefinitely, each of us would have had since the time of the birth of Christ a number of ancestors represented by $(2)^{57}$, or about 120 quadrillions—a number far greater than the entire human population of the globe since that time As a matter of fact, owing to intermarriage of cousins of various degrees, the actual number of ancestors is much smaller than the theoretical number For example, Plate says that the late emperor of Germany had only 162 ancestors in the tenth ascending generation, instead of 512, the theoretical number

"Davenport concludes that no people of English descent are more distantly related than 30th cousins, while most people are much more closely related than that If we allow three generations to the century, and calculate that the degree of cousinship is determined by the num

ber of generations less two, since first cousins appear only in the third generation, the first being that of the parents and the second that of the sons and daughters we find that 30th cousins at the present time would have had a common ancestor about one thousand years ago or approximately at the time of William the Conqueror As a matter of fact most persons of the same race are much more closely related than this and certainly we need not go back to Adam or even Shem, Ham, or Japheth to find our common ancestor '

Galton's data in the light of genetics —The two main laws of Galton seem to us, in the light of our present knowledge of genetics to be peculiarly barren The laws are true enough, but throw little or no light upon the mechanism of heredity They and the laws of Mendel are not contradictory in fact each type of laws could be transmuted into terms of the other The main differences between Galton's and Mendel s laws of heredity are (*a*) that Galton's laws do not distinguish between genotypic and phenotypic differences, (*b*) character differences are often not capable of being arranged in graded series at all but are qualitatively different and without intergrades, thus being unsuitable for statistical study (*c*) the statistical method often loses sight of the exceptional cases, which are usually the most interesting and instructive

On the whole, it may be said that Galton s work is now considered as chiefly of historical value It served a useful purpose mainly in that it definitely called attention to the fact of heredity in man, a fact that was at the time hardly recognized in political educational, and sociological circles

CHAPTER XXXVII

TWINS AND HEREDITY

I THE BIOLOGY OF TWINS

Twins have always been a source of interest and amusement to other people There is something inherently comic in the existence of two individuals so similar that their identities are likely to be con fused Stories and plays have been written, the chief plot of which involves the mistaken identity of two brothers, two sisters or a brother and sister Quite recently I came to know an attractive lady who told me an interesting story of her girlhood—a story from real life that bears out those of drama and fiction This young woman had a sister so much like herself that her best friends could not tell them apart It so happened that a young man became attracted to one of the twins and called practically every night to pay his court This assiduous wooing soon became burdensome, and, to relieve herself, the young lady had her twin sister substitute for her on some of the evenings In the course of time the young man approached a proposal of marriage but unfortunately selected an evening for popping the question when the substitute twin was on duty He told her that, though some claimed to see no difference between her and her sister, he himself thought there was a great difference and all in her favor He said he could not see why other people thought them so much alike The substitute was forced to confess the deception, but in spite of this, the young man insisted that she was the one he wanted, and suspected her of merely testing his fidelity In the resultant confusion the young man made such an ass of himself that neither twin had any further use for him

This is, however not to be a romance about twins, but a serious discussion about the scientific value of twins, so let us get on with it

Various kinds of twins —Several different kinds of human twins are recognized among which the most significant are identical (dupli cate) twins, "Siamese twins," and fraternal twins Duplicate twins are, as the name implies, extremely similar in their personal charac teristics (Fig 91) They are always of the same sex in a pair, have the same or very similar temperaments, dispositions, and mental ca pacities They are believed to be derived from the division of a single zygote There is no such reality in nature as that useful and romantic

type of twin in which brother and sister are so much alike that one may take the place of the other Such twins are purely literary significance and justified only for dramatic and fictional purposes

Siamese twins are of the same origin as duplicate twins They are the product of the division of a single individual into two but in their case the division has been incomplete Sometimes they are double in the head region and single back of that sometimes they are double in the lower trunk region and single anterior to that and



FIG 90—A pair of typical fraternal twins showing differences in eye color features body build etc

sometimes they are double in the head and leg regions and united only in a small area at the hips or sides Cases of Siamese twins that survive are exceedingly rare the number recorded being so small that they could be counted on one s fingers Yet it has been my privilege to have examined within recent years two of these cases

Fraternal twins are quite different in origin They arise from the simultaneous fertilization of two eggs and except that they develop together in the same uterus, they have no closer kinship than ordinary brothers and sisters They may be of the same sex or of opposite sexes in just the same way that families of two children may be both boys, both girls or a boy and a girl Fraternal twins are therefore,

only about as similar as ordinary brothers or sisters A typical pair of fraternal twins is shown in Figure 90

The origin of identical twins —While there is no doubt in the minds of biologists that human identical twins are derived from the division of a single egg or embryo, it has never been possible to demonstrate this directly Early stages in the development even of ordinary single human embryos are exceedingly rare, and there are no specimens



FIG 91 —A pair of typical identical twins, showing no genetic differences.

known that are young enough to show the beginnings of normal twinning Hence our belief that identical twins come from a single egg is based on a mass of indirect, but none the less conclusive, evidence

In the first place, it so happens that the entire developmental history has been worked out for another mammal, the nine-banded armadillo, an animal which bears one-egg identical quadruplets at nearly every birth (see Fig 52) The peculiarities of both egg and uterus are very similar to those of man The known steps of embryology of the two species accord so closely that it is believed that the

process of twinning in man must be essentially the same as in the armadillo Now, in the armadillo, every step in the double twinning process has been observed, and we have some rather well supported theories as to why the egg divides into four individuals instead of developing into but one There is in the armadillo a well-defined hitch in the process of the attachment of the young embryo to the membranes of the uterus For a month or more after the embryo descends the egg tube into the uterus it lies free in the uterine cavity, whereas it should normally have attached itself immediately to the maternal tissues so as to receive food and oxygen from the maternal blood During this period the young embryo is completely stopped down and is unable to develop at all Its vitality becomes so lowered that, when finally the mechanism of attachment does right itself and the embryo is afforded the chance to feed and respire, the fires of life have burned so low that the embryo cannot maintain its unity, but starts to develop first at two regions and then at four These four growing points develop into the four separate embryos

That a lowering of the rate of vital activity during early development is able to induce twinning has been demonstrated experimentally in several species of animals, notably certain fishes and echinoderms Apparently some embryos cannot maintain their singleness under conditions that lower vitality On this account right and left hand sides cease to co-operate to form a single individual, and each half grows independently into a whole embryo In armadillo quadruplets, some hundreds of which have been examined, there are frequent cases of mirror imaging, that is, peculiarities found in the right side of one twin occur on the left side of the other Again, it has been found that armadillo quadruplets are about 90 per cent identical on the average, and are always all of the same sex in a litter

Applying these known facts to the case of human twins, we find the following correspondences Identical twins in man average about 90 per cent identical, they are always of the same sex in a pair, they show frequent instances of mirror imaging Thus, in about one third of the cases one twin is right handed, the other left handed, also in about one third of the cases the whirl of hair at the crown is clockwise in one twin counter-clockwise in the other Minor peculiarities of features—skin, teeth finger prints and palm patterns—are commonly on opposite sides of the two individuals. In addition to these evidences for the one-egg origin of human identical twins, it should be said that many prenatal human twins have been observed by obste-

tricians and these show peculiarities in embryonic membranes similar to those of armadillo quadruplets Thus it will be seen that the human twinning situation rests largely on the armadillo quadruplet situation

As to the causes of human one egg twinning, we have no positive knowledge It seems probable, however, that the cause is somewhat similar to that described for the armadillo Some early hitch in the normal correlation of embryonic and maternal physiological relations, involving a delay in placentation, is believed to be responsible for twinning in man Technical studies of tubal pregnancies strongly support this view, but lack of space forbids the introduction of this testimony

In concluding the discussion of the causes of human twins, it must be admitted that as yet we do not know enough to enable us to control or to permit the production of twins So we can give no practical advice to those who desire to have twins or to avoid them

II THE TWIN METHOD OF STUDYING HEREDITY IN MAN

In recent years there has grown up a new method of studying heredity in man by making use of twins, and especially of identical twins A number of European workers, notably Siemens and von Verscheur, have written extensively on this method and have contributed many new facts about the heredity of pathological conditions and normal peculiarities in man

The validity of the method rests on the ability of experienced students of twins to diagnose twins accurately as to whether they are identical (monozygotic) or fraternal (dizygotic) Both Siemens and von Verscheur are confident of their ability to do this, and I fully agree with them, having had no real difficulties in making this diagnosis in considerably more than a hundred cases

Assuming that the two types of twins can be accurately separated by experts how can twins be used in determining what characters are hereditary? The working hypothesis is that those characters that are the same in all cases of identical twins, but are usually different in fraternal twins, are hereditary, and that those characters that are different in identical twins, or that occur in one such twin and not in the other, are non hereditary Now there is one weakness of this hypothesis, namely, that some undoubtedly hereditary characters actually do express themselves differently in the two individuals of a monozygotic pair This is not surprising, for often in a single individual a hereditary character may express itself on one side of the body

and not on the other or else it may express *itself much* more exten sively on one side than on the other For example there are certain finger print and palm print patterns that may occur on the right hand of an individual and not on the left or may be present in one form on one hand and in another form on the other hand Now if identical twins are derived from the separated right and left halves of an em bryo that typically would produce a single individual such twins may be expected to be only as similar as are the two sides of a single indi vidual In view of this circumstance we would be inclined to modify the working hypothesis of Siemens to the extent of saying that charac ters which are always the same in both individuals of a pair of identical twins are undoubtedly hereditary but that the failure of certain characters to be the same in both members of a pair does not prove that such characters are non hereditary That this point is well taken is demonstrated by a study of armadillo quadruplets which are un questionably monozygotic In these animals it frequently happens that a well defined peculiarity such as a local doubling of a band in the armor of the back a rare anomaly known to be inherited from the mother does not appear in all four offspring from a single zygote One of the four may have it on the right side another on the left side a third on both sides and a fourth may fail to show any sign of it Yet it would be foolish to claim that because the character fa led to appear in one out of the four quadruplets such a character is non hereditary

Using the working hypothesis however in its original form Sie mens has been able to show that a large number of pathological condi tions are hereditary He has specialized on birthmarks (naevi) and has shown that various types of naevi constantly appear in both twins if they appear at all He has shown that even moles and freckles are hereditary

Bonnevie Wilder and I working independently have shown that various *peculiarities of finger prints and palm patterns are hereditary* This has been done by the method of determining the coefficients of correlation between right and left sides of the same individual Com parisons of the extent of correlation in identical twins is made with those in fraternal twins sibs and unrelated persons For example I have studied statistically the numbers of ridges in the finger patterns of fifty pairs of identical and of fifty pairs of fraternal twins and the coefficients of correlation obtained are as follows

COEFFICIENTS OF CORRELATION BETWEEN TOTAL RIDGE COUNTS OF FIVE FINGERS OF EACH HAND

Correlation between right and left hands of same individual	$r = 0.93 \pm 0.01$
Correlation between right plus left hands of identical twins	$r = 0.95 \pm 0.01$
Correlation between right plus left hands of fraternal twins	$r = 0.46 \pm 0.08$
Correlation between right plus left hands of 30 pairs of brothers and sisters (Bonnevie)	$r = 0.59 \pm 0.08$
Correlation between right plus left hands of 30 unrelated individuals (Bonnevie)	$r = 0.27 \pm 0.12$

It will be seen that identical twins are even more alike in total ridge counts of finger patterns than are the two sides of the bodies of single individuals This is in itself strong proof of the hereditary character of finger patterns Fraternal twins are no more alike (in this series not as much alike) as are ordinary sibs The extremely close resemblance between identical twins should be contrasted with the very low correlation in unrelated individuals The slight positive correlation in unrelated individuals may be taken as a residuum of racial heredity

In contrast with finger patterns, which everyone knows are fixed at birth and do not change throughout life—a fact that makes them valuable as an aid in personal identification—let us examine the degree of correlation in mental qualities as exhibited by groups of varying grades of relationship Taking the Intelligence Quotient (I Q) as a measure of mental capacity, the following table was worked out by Kohn, a capable German student of twins

COEFFICIENTS OF CORRELATION BETWEEN INTELLIGENCE QUOTIENTS (I Q)

Identical twins	0 90
Fraternal twins	0 59
Sibs	0 50
Sisters	0 47
Brothers	0 46

It is highly significant that mental differences show substantially the same grades of correlation as do the finger patterns, which are generally admitted to be purely hereditary Various other authors, including our own local investigators, have found essentially the same

situation Moreover we have found that in identical twins the more alike they are physically, the more alike they are mentally These studies tend to show one thing most clearly, that there is no distinction as to heredity between physical and mental characters

A great many reports have come in from clinics all over the world concerning cases of identical twins in which both show rare and peculiar physical anomalies Only a few examples can be given out of a large number that lie before me

Bruce and Daugherty report seven cases of identical twins both afflicted with the same form of diabetes mellitus Kelly Hale reports a pair of twins both afflicted with congenital dislocation of the hips one with left hip dislocated and right eye crossed the other with right hip dislocated and left eye crossed This is a case of pronounced mirror imaging and shows an unusual association of characters Meierowski reports a striking case of identical twins both with unilateral strabismus one with right eye badly crossed and the other with left eye slightly less crossed Croon reports a case of a pair of identical twins who began menstruation on the same day were normal until thirty, then suffered alike from menstrual difficulties Both had menopause at fifty and three years later both developed the same type of carcinoma of the uterus Von Verschuer reports a striking case of inguinal hernia (rupture) in a pair of elderly twin men in which the rupture appears on the right side of one and the left side of the other Goldstein and Schenck report an unusual case of dwarfism in twins The smaller of the twins was smaller in all organs on one half of the body, a case of hemihypertrophy Ahlfeld reports seven cases of twins in which similar bodily malformations were present in both members of a pair D Outrepont reports a case of twins of which both had *spina bifida* and both had six fingers or six toes on each limb Lehmann reports cases of twins both afflicted with cerebral hernias and hypospadias Davis reports six cases of hare lip and cleft palate present in both members of the twin pairs Parker reports two cases of twins both of whom developed dementia praecox at nearly the same age Bradley reports several cases of twins both afflicted with similar forms of manic depressive psychoses Gesell reports twins who both showed extraordinary precosity, who sat up at six months walked and talked at eleven months learned French at three years and were in the seventh grade at the age of nine

No one has ever taken the trouble to get together all the data reported by observers of twins If we had all this information together

in available form, it would doubtless constitute a most valuable contribution to the study of human heredity The twin method is a new one and not yet so well established as the others, but it is growing in favor every year

III CRIME AND DESTINY

One of the most remarkable uses of the twin method in the study of heredity has to do with the problem of the heredity of criminal tendencies Professor Johannes Lange, of Munich, has recently reported the results of many years of work on the criminal records of twins one or both of whom had been in Bavarian prisons or reformatories This work was a part of the program of research of the Bavarian Institute for Criminal Biology, and is held in high esteem by leaders in the field Lange s book entitled *Crime and Destiny* reports in some detail the criminal records of thirteen pairs of identical twins and seventeen pairs of fraternal twins, one or both members of a pair being in every case a confirmed and inveterate criminal But what about the other twin in the two groups? The answer to this question is astonishing Of the thirteen pairs of identical twins, there were ten cases in which the other twin of the pair was also an equally confirmed criminal Not merely this, but the twin criminals of each pair exhibited the same types of criminality both were swindlers, both thieves both sex offenders both drunken ne'er-do wells, etc , though in no case were the two members of a pair associated in their crimes Of the three pairs of identical twins in which only one was a criminal there were two cases in which one member of the pair had suffered a serious head injury at birth or in infancy, which might well have been responsible for his criminal tendencies, while in the remaining case one twin suffered severely from a goiter which might have profoundly affected his conduct From Lange's description of the last case, however, it seems highly probable to me that this case is incorrectly diagnosed as identical, but Lange leans over backward in his attempt to weight the evidence against the conclusion that criminal tendencies are hereditary

In contrast with this impressive study of identical twins, is that of the seventeen cases of fraternal twins, of which there were only two cases in which both members of a pair were criminal and these exhibited relatively mild forms of criminality, such as might not have appeared at all in a more favorable environment

In one of the cases of identical twins, both of whom were criminal, one twin, after a long criminal record, married a good woman of strong

character who encouraged him to stop drinking and smoking and helped him to become a fairly useful member of society. This case tends to show that there is an environmental element in crime, but the point of the whole study is that there are certain hereditary types of mind that yield more readily than others to the ordinary social conditions that lead to crime. In this sense, and in this sense only, may it be said that criminality is hereditary.

IV. TWINS AND THE RELATIVE POTENCY OF HEREDITY AND ENVIRONMENT

Two sets of factors are involved in the development of an individual, and doubtless the same two sets of factors are responsible for racial development, or evolution. One category of factors is intrinsic and seems to depend upon the physical organization of the germinal protoplasm or upon the mechanisms that are involved in cell multiplication and differentiation; all such factors are here included under the term "heredity." The other category of factors is extrinsic and seems to involve both environment and training; these factors are usually included together under the term environment. The controversy as to the relative importance of these two sets of factors is so old as to be time-honored. In the case of man especially the question as to what characters are due to nature and what to nurture has long been an active issue.

Before the rise and growth of democracy the opinion was very commonly held that man was born noble or base, with high qualities or low, according as he came from good or bad stock. The various well-defined strata of society were believed to have a basis in blood. Blue blood was the criterion of nobility or of high character. With the rise of democracy, however, the view has come to prevail that all men are created equal and that inequalities arise only as the result of inequitable distribution of environmental and educational advantages. This has been until recently the prevailing opinion in educational, sociological and political circles. This view, ignoring hereditary differences and overemphasizing of the potency of environment, has caused the pendulum to swing to the opposite extreme.

The present century has seen such a surprising advance in our knowledge of the laws and the mechanism of heredity that it is no wonder that biologists have come to feel that heredity is far and away the chief factor in human development and that environment and training are only minor modifying factors.

In one sense the controversy about the relative importance of heredity and environment is rather silly and futile for both heredity and environment are absolutely essential for development to take place at all The real controversy hinges on this question *With respect to any given character do the actually existing differences in heredity have a greater or a less effect in determining the differences found in the adult than do the actually existing differences in the environment?*

Now some characters such as eye-color hair color shape and arrangement of teeth finger and palm patterns features body build and a long list of others are evidently not much altered by existing differences in the environment and may therefore be called purely hereditary—and by this we do not mean that the environment has nothing to do with their determination Other characters such as body weight muscular development skills of various kinds extent of tanning of the skin certain types of eye defects effects due to the ravages of disease and many others seem to be very largely influenced by existing differences in the environment and may be called environmental Large numbers of characters fall in between these extremes characters that are surely predetermined within limits by heredity but are also much modified by actually existing differences in the environment Among the most significant types of human difference that are both hereditary and environmental in the sense just discussed are differences in mental capacity (as determined by intelligence tests) and differences in temperamental and emotional make up (as determined by psychological tests)

Identical twins have furnished some highly significant data on this point As a preliminary step it was necessary to determine the average differences in mental capacity and in temperament for fifty pairs of identical twins reared together and for the same number of same sexed fraternal twins reared together Since the heredity was the same and also the environment essentially the same for identical twins reared together the observed differences must be due largely to the workings of the asymmetry mechanism the same mechanism that makes the two halves of a single individual different In order to test the effect of differences in environment, therefore we must compare the differences found in identical twins reared together with those of identical twins reared apart In both those reared together and those reared apart the asymmetry mechanism works in the same way therefore greater differences in separated twins than in those reared together may fairly be attributed to differences in environment

Now scientists cannot cold bloodedly separate identical twins in infancy and rear the two under radically different environments, but fortunately this very thing has sometimes been done for them without their knowledge. When by a stroke of good fortune we are able to locate such cases, we have before us a scientific experiment completed and only needing to be studied. During the last few years we have completed the study of five such cases. A brief account of these five cases, (one studied by Muller and five by Newman) may interest the reader:

Muller studied a pair of twin sisters, left orphans and separated at two weeks. They did not meet until they were eighteen years old. They lived under somewhat similar social conditions in northwestern mining and ranch country, but there were marked differences in their educational and social experiences. Physically, although entirely separated from infancy to adulthood, they were as identical as are identical twins reared together. Their heights, weights, features, teeth and finger nails, eye color, hair color, glove size, blood group etc., were indistinguishably similar. In addition both were left handed, both had the same peculiar prominences on the ankles, and both had a droop of the mouth on the left side. Both had had two or three attacks of tuberculosis almost simultaneously. Intelligence tests showed them to be both very bright, and their scores were as similar as those commonly made by the same individual taking the tests twice over. In the temperament and emotional tests, on the other hand, they showed a very wide divergence, as great or greater than those between two individuals taken at random. In this case the environmental differences had left the physical and intellectual characters unmodified, but had produced a profound effect on the emotional nature of the twins.

Newman's first case consisted of a pair of twin sisters separated at eighteen months. One was taken to Ontario, and the other remained in London, England, where they were born. After seventeen years of complete separation, the English twin joined her sister in Canada where they now live in a pleasant medium sized town. Their environments were very different during the period of separation, as different as one is ever likely to find in cases of separated identical twins. One was reared in a congested district of London and passed the trying period of the war there, the other lived under good circumstances in a suburban town in Ontario, and did not feel the pressure of war conditions. Their educational careers were equal in amount and kind

Tests showed however, that they were very different in mental capacity the Canadian twin being decidedly the brighter of the two The difference was three times as great as the average difference of fifty pairs of identical twins reared together, and even somewhat greater than the average differences of fifty pairs of fraternal twins reared together Physically, the Canadian twin was much superior, weighing 102 pounds as compared with 92 for the English twin, a great difference for such small persons They were strikingly similar in height, build, features hair and eye color, and finger and palm patterns Also, they showed great similarity in their will temperament qualities and in emotional reactions Thus the differences in environment had caused marked divergence in the physical condition of the body and in mental capacity, but had left the emotional nature unmodified In every respect this case is the direct opposite of Muller's case

Newman s second case consisted of two twin sisters, who never heard of each other until they were about twenty-one years of age, but came together through the lucky accident of an acquaintance of one accosting the other by mistake They were separated at eighteen months, adopted by two different families, reared in much the same *stratum of society*, but one had only grade school education, while the other went through secondary and normal schools and taught grade school These twins were physically almost complete duplicates when examined, as similar as the most similar identical twins reared together The mental tests showed that the more highly educated twin ranks far above her less educated sister, the difference being more than three times as great as the average difference of fifty pairs of identical twins reared together and even greater than the average difference of fifty pairs of fraternal twins reared together In contrast with this stands the fact that in all tests of emotional traits and of temperament, the twins give the impression of being remarkably and unusually similar To summarize, these twins show a profound effect upon mental capacity due to vastly different educational careers, but physically and temperamentally they are nearly identical

Newman s third case consists of two young men, one of whom lived in fairly large cities and the other in small country towns and villages They had been separated at two months and had never met until they were about twenty two years old, when one discovered that he had a twin brother while looking over some old papers By a little detective work he located him Their educational experiences were

nearly the same, the city twin having perhaps slightly better training When examined, they were very similar in all genetic characters, but the city boy was in much better physical condition, weighing over 10 pounds more than his brother, though they were both small persons In mental capacity the city boy was, on the basis of most of the tests given, definitely superior, though they were nearly equal on the Stanford Binet test In will temperament and emotional tests they were very far apart, as far apart as were Muller's twins in this respect In summary, this pair shows marked differences physically, mentally, and temperamentally, but more pronounced differences in temperament than in either of the others

Newman's fourth case concerns itself with a pair of young women, now twenty nine years of age, separated at five months and reared in different families in the same part of Ohio One was reared entirely on a farm, while the other lived mostly an indoor life in a town The town girl had grade school and high school education, the farm girl only country grade school training They were almost identical physically until about twelve years ago, but now the farm girl is in far better physical condition, weighing 138 pounds as compared with 110 pounds for the town girl, and being very much stronger and more vigorous The town girl had a mental rating much higher than her sister, the difference being over three times as great as the average difference of fifty pairs of identical twins reared together and considerably greater than the average differences of fifty pairs of fraternal twins reared together In will temperament and emotional reactions they are extremely different, as far apart as were Muller's twins or Newman's third case In summary, these twins were about equally different in physical mental and temperamental characteristics

A fifth case is being studied just as this revised edition goes to press It concerns itself with a pair of twin women now thirty eight years old separated at three months They did not know of each other's existence till they were sixteen years old A preliminary study of the data shows rather close similarity mentally and temperamentally, but a great difference in physical condition

It is still too early to attempt to draw general conclusions on the basis of these six cases, but some facts confront us that cannot be dodged Perhaps the most disconcerting fact revealed by the data is that *fraternal twins reared together are on the average somewhat more similar in mental rating, as judged by intelligence tests, than are identical twins reared apart* This seems to mean that when heredity is different

and the environment the same, twins tend to become more similar than when the environment is different and the heredity is the same Extreme environmentalists may see in this situation evidence that environmental differences are more powerful in determining mental capacity than are hereditary differences I do not believe that this is true, and for several reasons In the first place, if environment were more powerful than heredity, identical twins reared together should not be twice as similar as fraternal twins reared together, yet this is the case In the second place, all the tests used to determine mental ability, except possibly the International test, measure largely the effects of training This tends to mask or cover up hereditary resemblances and differences, increasing the difference in cases where educational experiences are widely divergent and decreasing the differences (in fraternal twins reared together) where educational experiences are alike Thus the tests used tend to exaggerate the potency of environmental differences and to minimize the potency of hereditary differences

In spite of these weaknesses in method however, the data at least warrant the conclusion that both hereditary differences and environmental differences play important rôles in determining mental characteristics In so far as a person's mental status is measurable in terms of ability to perform well or poorly on intelligence tests, it seems fair to conclude from our data that differences in heredity and differences in environment are about equally responsible for the mental status of an individual On the other hand, since a large part of what is measured by intelligence tests is merely achievement and not real mental capacity, some will say we are not really measuring mental status at all There is doubtless some justification in this criticism of intelligence tests, yet I cannot help but believe that one's individual mind, his mental rating is at any time the product of his hereditary make-up and his training If this be true, it is only fair to rate him according to this product

In spite of all this apparent evidence that hereditary differences and environmental differences are of about equal potency in determining mental status, I have a deep seated conviction, which I am unable completely to justify at this time, that differences in heredity are considerably more influential, perhaps twice as influential, in determining one's mental status, as are differences in environment

CHAPTER XXXVIII

DOES HEREDITY OR ENVIRONMENT MAKE MEN?[1]

ALBERT EDWARD WIGGAM

All men are born unequal When the Declaration of Independence made its pronunciamento, it was merely to serve notice upon King George that the American colonists were equal in their social, political and human rights to the citizens of England It was not meant as a scientific formula from some laboratory of psychology which had tested several thousand human beings and found them all exactly equal In all the common rights of man, the right to life, liberty and the pursuit of happiness, the world now concedes that one man is as good as another

But, when we study not men's rights, but men's natures and capacities, *nothing is more obvious than that all men are unequal, they* are born unequal, they will always be unequal, nature intended them to be unequal, and no system of government, social control or education has yet been devised or ever will be devised, that will make them equal Indeed, the astonishing and delightful discovery of modern psychology and biology is that the more you educate men the more unequal you make them The more you equalize opportunity, the more you unequalize men The more nearly you treat men alike, the more unlike they become It was Henry van Dyke, I think, who said that there is one thing in which all men are exactly alike, and that is that they are all different And the more you educate and develop these differences, the more they grow into larger differences

As a matter of fact, that is what education and good environment are for, to draw out and develop each man s individual and particular capacities and powers The old Romans invented the word ' education"—*educo*—a leading out of what was in a man, and not a pouring in of some magic fire from Heaven to melt and mold his soul into a likeness to other men *You can teach three boys the same knowledge* of history You can inform them of exactly the same facts of the past But I do not believe any school teacher in the world would maintain that he had filled them with the same spirit and viewpoint One boy

[1] Reprinted from *The Fruit of the Family Tree* Copyright 1924 by the Bobbs-Merrill Company

will be inspired by these facts to write historical novels and dramas, another will find them helpful in shaping economic and social legislation, while the third may remain almost wholly unaffected and devote his life to keeping a country grocery or to inventing a new method of making soap They all had the same facts the same teacher, the same school room But they all reacted differently, each according to his own ability and temperament—that is, his inborn make up

So an unalterable fact of human nature is that men are different The whole question at issue in this world-old heredity-environment debate is, what causes these differences?

All modern biology and psychology support the view that heredity plays a great part, and probably a preponderant part, in shaping a man's actions and reactions, his goings and comings, his health and happiness in this world We found in the chapters on twins and on the royal families that this is true But it may be of interest to present here some of the main *arguments* on both sides of this question, with these scientific discoveries as their background

It is commonly said that it is impossible to separate heredity from environment This is probably true when we consider merely one individual I doubt if we shall ever be able to determine whether a particular act by a particular individual, say whether he takes a drink of alcohol on some particular occasion or whether he commits a crime, is due to his heredity or to his environment. The causes are so hopelessly intertwined that no one so far as I am aware has presented the slightest hope of measuring the relative influence of the two forces *within the individual* As I have already pointed out in a foot note to a previous chapter, the Behaviorists—a school of psychologists founded by Doctor John B Watson—assert (at least some of the leading exponents of this school assert) that "ninety per cent. of a man's behavior is due to his environment"

This may be entirely true, but so far it seems to me it has not been removed from the realm of assertion into the realm of exact measurement. No one doubts that a man s early education is of great influence in determining his character and behavior in later life, but exactly *how* great—whether ninety per cent or twenty per cent.—has not as *yet so far as I am aware been measured And I do not believe* we can speak of percentages until we have measurements Environment *is* important in determining behavior, but *precisely how important* I doubt very much if we have any means at present for determining, when it comes to one individual, whether we consider one particular act or the

sum total of his character Indeed, it seems to me it would be pretty difficult to determine what one hundred per cent of a man s character really is, and when we had measured either ten per cent or ninety per cent of its total

I am inclined to believe from what Thorndike and his students especially Doctor Paul F Voelker, have proved as to the enormous influence of moral education and as to how much more we can influence the moral character than we can develop the purely intellectual traits, that by proper education and environment we could prevent nearly all individuals from committing actual crimes Crime is not itself inherited, because crime is a particular act by a particular individual And whether he commits that act, no doubt depends very greatly upon previous education, habits, the particular stimulus before him and all the forces of his environment. For all we know a man may commit a particular crime or take a particular drink entirely from environment And it may be that he can be prevented from these particular acts entirely by environment We know that moral ideas tend to diffuse themselves very widely over the mental life—or as the psychologists say, there is a very large "transfer of learning ' from one set of brain centers to others No doubt moral ideals set up wider transfers of learning and thus influence larger areas of behavior than the cultivation of particular mental abilities or aptitudes For this reason teaching a boy trustworthiness, as Voelker has proved, influences his conduct far more widely than teaching him algebra improves his proficiency even in algebra All of this is granted

What we know of heredity, therefore should not in the least discourage us (indeed, when deeply considered it ought to encourage us) from throwing every possible good influence about our youth The very stability of society depends on our doing this But when it comes to the question as to *which one of two individuals* is the more likely to commit crime at some time in his life or to take to excessive drink, we are in reality dealing with a different set of scientific problems. And when we come to the question as to which *family* is likely to have more members who, in any one age of the world, will be unable to adjust themselves to sound social behavior or who will easily be filled with aspirations for building a worthy character and maintaining *the social and political order, we are in a field where we can measure* the factors involved by fairly exact methods and predict results with considerable confidence

Doctor Charles F Goring, of the Galton Eugenics Laboratory of

London has shown in the most exact and elaborate study ever made of the influence of heredity upon the criminal tendencies of men—or what more technically is called the "etiology of crime"—that heredity is by all means the more important factor in the problem Some families easily react, naturally, to high social ideals, and some lack the foresight and the power to develop that true synthetic wisdom of life which we call in a general way self-control Education and environment will alter the weight and influence of these factors within each individual but I am not aware of sufficient evidence to prove that they will much alter the central tendencies either of such individuals or of such families

Perhaps Woods s illustration will illuminate this problem As he pointed out in 1912 at the First Eugenics Congress in London (the first time, I think this distinction had been made), it is only when we come to measure the differences between one or two groups of individuals, that we can really separate heredity from environment When we consider as Woods suggests, what causes a white man to be white or a negro to be black, or one person to have brown eyes and one blue, it is evident that these characteristics are the resultant of all the combined forces of heredity and environment We can not, therefore, by any means now known, separate the two sets of forces within any one individual But that the differences in pigmentation between the white and black races are almost wholly due to the differences in their germ plasm, no one can very well doubt True, a tropical sun will develop all the skin pigment a white man has the power to produce, and rearing a negro in a northern climate will reduce his pigmentation, but when placed in the same climate their differences are almost wholly due to heredity

Therefore we can not consider the heredity environment problem with much assurance of success, either in method or logic, unless we consider it as the problem of the differences among men And since as Thorndike pointed out long ago in his *Educational Psychology*, the prizes of life, whether of health or wealth or social position are nearly all relative matters, the result is that heredity is the most important factor in determining who shall secure these prizes and who shall not If the ideal of human health were an individual who could barely hobble about, then to attain this minimum of energy would be our highest ambition The healthiest man would be one who was almost helpless Health would still be, as it is now, a relative matter Just so wealth and influence are relative matters Among our ancestors a

man with a few shells or arrow heads was rich The fact, as Thorndike suggests, that Croesus and Rockefeller were the two richest men *in the world is due almost wholly to their superior natural powers over* those of other men to acquire wealth But the fact that Croesus accumulated only a few thousands, or at most a few millions, while Rockefeller has accumulated perhaps a billion, is almost wholly a matter of the differences in environment between the ancient and modern world

The differences among men, therefore, as I trust we have shown throughout this book, are almost entirely due to their differences in *natural* powers and aptitudes But none of this remotely discourages us from stimulating and educating those powers and aptitudes, nor should it discourage the individual from developing his own inner natural capacities and tendencies to the utmost To do this is the only way to attain *his* prize in life And whether he starts with one talent, two, five or a hundred, makes very little real difference We all regret that we do not have greater natures than we have I should really like to be such a man in intellect as was Plato or Pericles I should like especially to have the musical appreciation of Fritz Kreisler and the power to play the piano like Josef Hofmann But as William James pointed out, we can not be everything And to want to be everything is as foolish and as much a waste of good energy as it is for a dog to bay at the moon If we had everything we would probably lose that immense incentive of ambition and rivalry which, just because men are different, probably leads them to make nearly all the practical achievements and moral conquests of life

In his wonderful little book, *Talks to Teachers and Students*, James relates a story that goes to the heart of the problem He says that one day he had an old carpenter making some repairs on his house at Cam [illegible]

Josh Billings said, when a man starts down hill in this world, it seems that all creation is greased for the occasion However, the old carpenter finally made a remark which James states was one of the most profound observations upon human life he had ever heard or read in all the philosophies of men "There is very little difference," said the carpenter, "between one man and another, but, what *little* there is, is very important"

Have we not here the crux of the whole matter? I suppose, if,

when a baby Abraham Lincoln had been placed by the side of all the other babies in the world of that time, the best baby show judges on earth could have found very little difference between him and the thousands of others. And I am sure that if all the germ-cells from which these babies were born had been weighed and measured and analyzed and peered at through microscopes by all the biologists on earth, they could not have told which one would produce Abraham Lincoln. Yet existing somewhere, somehow, within this tiny microscopic cell which had been handed down to his parents and which represented his combined ancestry, were mighty and resplendent forces which ordained in advance that the child born from it would be one of the greatest human beings in all the tide of time.

But it will be said that the Civil War gave Lincoln his opportunity. Certainly it gave him this particular opportunity. No man could ask for a greater chance to serve mankind and enter among the human immortals. But the same opportunity existed for the four or five million other men who were born and grew up about the same time. The Civil War discovered Lincoln, but Lincoln *also discovered the Civil War*. Even the men in his Cabinet who had the stimulus of his overwhelming personality did not become Lincolns. Millions of men since then have taken him as their example and striven to be like him.

Of course we are all better because of the example of Lincoln. That is the value of a rich environment full of high ideals. I am a better man and so are you because this great soul lived and blessed the world. And I do not doubt that Lincoln himself was stimulated by his studies in the firelight of the lives of the men of the great generations gone. I do not doubt he tried to emulate them. Just in proportion to his own greatness does a man try to be like other great men. He does not try to copy them, he tries to expand his own powers in the light of their radiant examples. And I have noticed that the greater men are in real character, the more they have blessed the world with beauty and truth and happiness, men such as Lincoln and Washington and Foch and William the Silent and Gustavus Adolphus and Faraday and Huxley and Darwin and Pasteur and William James, the more nearly do they approach in their lives and personal characters to the Supreme Teacher—that other Carpenter who two thousand years ago also uttered some sayings that have changed the whole course of human history. Huxley, a thoroughgoing agnostic in philosophy, was almost fierce in his admiration of the character of Jesus.

As Professor Thorndike has pointed out, when it comes to the absolute achievements of men, the outward performance to which they can attain, environment is well nigh all powerful But when it comes to determining which individuals in that civilization will profit the most by it and contribute the most richly to its expansion and continuance the all important thing is each individual s heredity A man gives to his environment and receives from it just in proportion to the richness of his own nature Was any great environment ever built by a race of fools? No Was any truly small and mean environment ever built by a race teeming with genius? No Where there is no vision, no genius, the people perish

As another example, I walked down the street a while ago upon a pavement which took all the combined physics, chemistry, social, political and economic organization of a great industrial age to construct I had nothing to do with it It was a part of my environment. But I was able to walk faster and reach my journey's end earlier—that is, make a greater absolute achievement—because of it By my side walked a laboring man with a basket of groceries for his family Now, it may be that this man has a son in college who will some day write a much better book on heredity and eugenics than this one But it certainly would surprise me to find that all the students in colleges and all writers of books were laboring men's sons, and all the sons of the abler and more successful classes should to-morrow be handling the picks and shovels of our civilization

The whole point of this is that the things which men can do depend upon the tools that are at hand in the forms of environment, machinery, social organization, ideals and systems of education—in short, what we call the social heritage But the relative performances of one man as compared with another, that is, what each man does with these tools—this social heritage, depends almost entirely upon his individual, inborn heritage Consequently, it is the duty of all men to improve the general social heritage because this furnishes multiplied opportunities for each man to develop and express his personal heritage

Let us see if, in a rough way, we can not measure this The other day I motored through the western part of the state of New York, where I had learned the lives and histories of the farmers in consider able detail I was being driven by a man who knew them all intimately We passed a farm which a few years ago had been one of the model farms of western New York At the death of the owner, whom

we shall call John Crosby, its broad acres were divided into three equal shares for his sons Within three years the appearance of two of the farms had changed The fences were run down the stock was run down, the buildings were run down, while the weeds and underbrush had run up But on the third farm which fell to the youngest son the conditions were better than when the father died This son Joseph was rapidly acquiring the lands of his two brothers, William and Alexander The parts which he acquired promptly became models of successful tillage I have no doubt that, as the neighbors prophesied within a short time William and Alexander will be working as hired laborers for Joseph

Now here is a clear case where the environment remained unchanged, while the heredity did change and had a chance to reveal its overwhelming power All the stimulus was there for each one of the sons But only one reacted to it Any biologist would say in the light of his own studies, that Joseph was the only son who inherited his father s vigor and decision of character However they came by it no one could talk with the three brothers without discerning that they were radically different men

But let us drive on and see a like phenomenon on another farm We passed down the road and stopped in front of a large, handsome frame house Two different men had been on this farm within the last twenty years and "couldn t make it pay " It had grown up in thickets and underbrush, the buildings had become dilapidated, the fruit trees were wind broken and worm eaten, until finally a poor immigrant named Conrad from Switzerland had bought it for a song Within ten years he had developed it into one of the finest dairy farms in the region And when I looked at his five-thousand dollar Holstein bull and his prize cows giving from ten to fifteen thousand pounds of milk a year, I thought on the one hand of what glorious achievements American environment permits men to make, and on the other of what a small percentage of the millions of job hunting immigrants America has admitted in the past forty years could do as well as Conrad Had we had the wit to select and admit only the Conrads and the Joseph Crosbys, what a glorious future for our country! What wonderful cows, what splendid hogs, what brilliant poets, painters, inventors politicians and statesmen would fill this country for all the generations to come!

It always straightens out this whole tangle of heredity and environment for me to think of two boys I knew in a western state—let us

call them George and James. There was no great outward difference in them as boys Their parents tried their utmost to treat them exactly alike, but the more they treated them alike, the more amazingly unlike they grew When their mother sent them on an errand James would always loiter and show up an hour late, while George was on time. George was always devising new ways of doing the farm work, while James was content to get by in any old way or not get by at all.

When they went to school the teacher saw no great difference between them, but soon discovered that while James was two years older, still, George could do his class work better and within a year was one grade ahead of his brother In spite of expending very little effort on George and every possible effort on James, it was impossible to make them progress alike. Of course two or three hundred years ago James and perhaps George also, might have been mere ignorant louts about the village Quite possibly both might have been bandits and criminals according to the ideas of crime in that day But if so, George would have been the leader and James the follower Consequently the absolute mental and moral achievements of both were enormously increased by the wonderful modern environment. But their achievements and character remained relatively the same

However, the community saw no outstanding differences between these two boys They were both good, well behaved lads But let us look thirty years later George was in the United States Senate, one of the great orators, one of the great political and economic thinkers of our time, one of the keenest and most graceful writers of the day and, had he not made a political blunder, would probably have been president of the United States, while James was keeping a fourth class pie counter in western Illinois

Now this world is made up of Jameses and Georges And in the careers of these men and these families, the Crosbys, and the Conrads, the Jameses and Georges, are exhibited in simple relief the vast forces that make and unmake empires, that create and separate social classes, that evolve great cultures and intellectual disciplines and overthrow them—in short, the forces that make our lives, and make history and civilization what they are. I might add that George married into one of the great families of the world and his two children show promise of helping to glorify the age James married a woman of his own type and his two children show every promise of continuing in pie-counter channels. Now it is necessary to have pie counters as well as Senates And I have little doubt that James blames his situation on his environ-

ment or upon "bad luck," or complains that "things went against him" We all blame our misfortunes upon something or somebody else and lay our successes to ourselves

The inspiring thing about all this to me is that it gives us such an exalting view of life It proves, not that we are slaves, but that we are masters of our environment Look back at your own schoolboy or schoolgirl friends Have they not all carved out their own fortunes in the main? Have they not all developed about as you would expect from your own intimate knowledge of their natures, their heredity? The point is, have they not selected chosen and built their own environments? There are seeming exceptions but is not this the general rule? It would fill me with despair if I thought that enviroment was the main shaping influence of my life It has some influence on my character, and immense influence on my outward career, but if it had the overwhelming power that many people ascribe to it, the power to change my fundamental *character* then I should not have the slightest idea what sort of man I would be twenty years from now I have not the slightest fear of the future because I know that my environment and above all my own inner character are mainly in my own hands I might be thrown to-morrow among criminals I have not the slightest doubt that if I were I would begin at once to try to reform them, probably without great results But if I am the mere victim of my environment I have precisely the same mathematical chance as any criminal has, of committing murder and being hanged within the year

Do you suppose that your grandchildren are going to be the victims of their environment as far as their inner characters and mental capacities are concerned? Wars may disrupt the nation Civilization may go to pieces But if you marry the right mate and endow your children with your own royal nature and your marked abilities you may be sure they will rise amid its ashes and build a great and heroic life

I have no doubt that there were great men among the cave men But they lived a poor and mean life In a poor environment men must live a poor life, as we look at it, although men always find excitement interest and adventure under any set of circumstances We see that in the case of our Puritan forefathers Compared to the great buildings, laboratories and libraries of Yale, Harvard or Columbia their little log academy looks poor indeed Yet I doubt seriously if the men within this little structure lived a life of less mental excitement or of less true inner glory

As Karl Pearson has said, "It is man who ... ment, and not environment that makes the ... main, this is true, it is not altogether true ... profession is often seemingly a matter of ... read a sentence in a book thirty years ago ... cause of my devoting my life to the study of ...

ambition to be a professional scholar of ... me a heredity, an inner urge, to do the ... science and in lecturing and writing for my ... stop this inner urge any more than I could ... fork.

Of course people always say, "But don't ... children from the slums and do wonders for ... You can do a great deal for them But you ...

Many children from the slums rise by their ... ornaments to our civilization This proves ... heredity into bad environment and not ... people are ...

tage of poorly endowed, mentally, morally ... say, the poor heredity—in the slums than ... the product of many injustices in our social ... tions, but if we have slums, it is those with ... main, fall into them

To test this, go if you will, into some small ... region It would surely seem that there ... all, every tub stands on its own bottom, ... want. I was in one town in Iowa where they ... the poor But the preacher told me he did ...

cess-pool dirt in the lowest sections of New York. The "settin'-room' was properly named, for they seemed to do nothing but just "set."

Now honestly, my uplifting environmental friend, what *can* you do for such people? They had plenty of money and ample opportunity They went to picture shows, and their children attended, or rather were forced to attend, school "The old man" got three to ten dollars a day The farmers about the town were crying for tenants, and willing, practically, to set a man and his family up in business if they would only properly till the land But their poverty was pure biological poverty, inborn, ineradicable Their real poverty was poor heredity And do you suppose that if those people drifted into the larger cities they would build residences on the avenue, or would they simply fall naturally into the slums? Many a strong man goes into the slums, under the wicked crush of modern industrialism But such *stock* does not long remain there Many of the children or the grand children fight their way out. The vast slums of the world are in the main inhabited by breeds that have been there for centuries Sydney, Australia, has probably the largest slums relative to its size of any city in Anglo-Saxon countries The belief of Doctor Charles B Davenport who investigated it, is that this is largely due to the fact that Sydney was originally settled chiefly by criminals and lower stocks deported from England one hundred and fifty years ago Anyone who will read the account of the character of these shipments of slums stocks which England sent for many years to Sydney in ship loads, as given in the *Encyclopedia Britannica*, will, I think, be impressed with the high probability of the truth of Doctor Davenport's conclusion

We have seen then that heredity is the preponderant factor in the relative character of men, and almost the whole factor in mental capacity, and that our success as compared with that of our fellows is largely a matter of our natural endowments But the real lessons that emerge for us all are, first, that you "can't make a silk purse out of a sow's ear", and second, that human success and human happiness are largely relative things "We are not trying to get ahead in this world," as Professor Thorndike says, "but to get ahead of somebody' To be the most beautiful girl in the county is beauty enough The most beautiful girl in Podunk feels no envy of Agnes Soret, long the reigning beauty of France I suppose President Wilson and Theodore Roosevelt were eager to get ahead of each other But you and I never gave a thought about getting ahead of either one of them The third

conclusion is that environment does not much change the relative situations and achievements and characters of men But a rich environment gives *all* men the chance for greater achievements and a wider life If Roosevelt had been born in Africa he would not have been the Roosevelt he was But even in Africa he would have been the "Buanna Tumbo"—the big hunter as the natives called him, the mighty man with the big stick with the power to move things and men And he would have had a ' perfectly corking time "

You should remember always that by the hereditarian view you are not mastered by fate, but you are *the masters of fate* You make your environment to a far greater extent than it makes you Life is self expression, self realization Every one should study his heredity, and the lives of his immediate ancestors He should choose his vocation with a view of avoiding their failures and imitating their successes If they drank to excess, it should be a special warning If they had particular talents, these should be emulated You probably have some or all of them Let your natural, inborn light shine, to be seen of all men You are *always going to* live with yourself Then make yourself a good person to live with You probably have a great deal of good heredity going to waste Explore yourself and find out You can not express anybody else's heredity You must express your own For there is no antagonism between heredity and environment Heredity has furnished you with untold powers and no one ever develops all of them as much as he could and ought It is your duty to use those powers in building an environment amid which and with which both you and your descendants may make the noblest possible practical achievements

It seems to me that this view of life, far from being fatalistic, as the extreme environmental view surely is, is filled with the most inspiring optimism A boy may never hear the chance sermon, or read the inspiring book which our environmental friends often point out as being the "cause' of his fine career in life If such things are the "causes" of the success or failure of men, then we are mere pawns upon the chess-board of environment, mere marionettes upon the stage whose wires are pulled by this mysterious and awful hand of doom In a bad environment a boy would be bound to turn out to be bad, and in a good environment he would be bound to turn out to be good Whatever the optimism or pessimism of such a view may be, we see simply that this is not true Good boys constantly come up out of bad environment, and boys turn out badly amid the best environment that human wisdom can devise.

But the thing to reflect upon is that every child who is not positively idiotic has within him those glorious powers by which he can seek out the inspiring man who will preach to him the inspiring sermon, he has the power to seek out the good book and read it, he has the power to choose his companions, his teachers, the way he spends his time and money, and in the long run build his own surroundings

Obviously, however, even here environment plays a very strong hand, for the more choices that are opened before a child, the more it is encouraged to make this choice instead of that, the more surely will it be enabled in the end to form those *right habits of choosing* the good instead of the bad, and also have those right objects and courses before it to choose which lead to self-mastery and success And self-mastery is merely success in the utilization of one's heredity For success itself by and by becomes a habit, ingrained in the very motor patterns of the nerve system itself Every child should be guarded against, and should guard itself against the habit of failure As James says, you may forget the fine resolution you made and failed to carry out, but the nerve cells do not forget Down in the very depths of our bodily organization, each tiny nerve cell is registering every act and thought, and laying it up in store for some future occasion, either for or against you "Make your nervous system," he says, "your ally instead of your enemy" This contains almost the whole basis of moral education And one should always remember with old Spinoza, the German philosopher, that "if you can keep from doing a thing because it is bad, you can keep from doing the same thing because something else is good" This is the whole difference between living the positive and the negative life One can not build a successful and happy life unless he has filled his mind and tuned his nerves to be up and alive with the things he *must* do, instead of always holding them back with the checks, inhibitions and prohibitions of the things he *must not* do The theological hell which is pictured for lost souls in the future, says James, can be no worse than the hell which many of us build for ourselves in this world by continually fashioning our nervous systems—our wills—in the wrong way And, granted that there is in us a power of choosing at all, granted that thinking has any purpose in it, then the opportunity to build daily more stately mansions for our souls in this world at least, is every morning opened anew to us all

Thus, notwithstanding our belief, and I think our demonstration that a man's inborn nature is the chief cause of his being different from other men, the cause of his making different choices, building a different "personality picture" of himself and his life, from the personality

picture of other men, our enthusiasm for environment continues as great as ever The poorest soil will increase its yield somewhat if fertilized but the same stimulus given to rich soil will increase its yield manyfold The one-talent man will improve a great deal by education, but the five-talent man will improve enormously This should be the chiefest source of comfort to the environmentalist himself—that the better the heredity upon which he expends his efforts the richer will be his rewards It takes all the skill of teachers trained in the best pedagogy in the world to teach some children to read and write, while other children practically teach themselves By doubling our educational efforts we would likely quadruple men's achievements, their generosity, integrity, courage, determination, and thus quadruple what Woodrow Wilson called "the world's fitness for affairs", but if we could double men's hereditary powers, their inborn virtue and excellence, the range and delicacy of their imaginations, the sweetness and charm of their personalities, and the exaltation of their natural desires, the humanism that would result—and what is civilization for except for a larger and finer humanism—would be beyond our power to foresee And this difference between the two alternatives that are always before mankind—the alternative of building either a better heredity or devoting all their efforts to building a better environment—is not a fanciful difference for we see always before us that some men have many times—Galton thought thirty times—as great natural endowments as have others Some men have in some directions a thousand or a million times greater powers than have other men

The millennium therefore, will be hastened by better education but it will be vastly more accelerated by better men And after all, is not this the final answer to the whole tangle of heredity and environment? Better social machinery will make better men and better men will enormously enhance the efficiency of the social machinery Our enthusiasm for environment will increase as we see more clearly through the improved education the modern world has given us how a well born race would use education for still more exalted ends

Instead, therefore, of being antagonistic, heredity and environment are reciprocal agencies, both placed at last by science within the grasp of man, by which he can lift his species out of the bloody sea [illegible]

to it It is an arduous highway, but its hardships need not be those,

as in the past, of the red tooth and claw of nature, but the striving passions of men to realize in richer cultures higher values for which to live

A rightly directed environment, not by brute death selection but by the happier method of birth selection, will improve man's heredity and in turn this better heredity will enrich the social heritage To instil the "will to believe" in a humanity naturally better than ours is as necessary an aim for education as to instil merely, as education does now, the will to believe in better conditions amid which humanity shall live Education will be doubly effective when it learns this great lesson

The ancient Greeks pictured ambition as a beautiful goddess rolling golden apples down the pathway of pursuing youth. Like these fleeting prizes the Eden of eugenics can never be attained But science and progress has at least stamped the picture of that Eden upon the imagination of mankind the Eden of a perfect humanity dwelling in an environment of paradise And, while it is unattainable *it is not a mirage* It is merely the great dream of human destiny and possibility which men began to dream back in that mysterious time when they started their organic journey from the jungle to their present high estate Only science and progress have drawn it for us in clearer outlines, drawn it nearer, and made it the conscious goal of the world s desire And while it can not be attained any more than Heaven can be here on earth attained, yet the passion for it, the going toward it the belief in it, the training and education of men for it, constitute that "new religion" of a better humanity which Galton said would "sweep the world" The goddess of humanity's ambitions can never be captured nor embraced, but as Thackeray said of the woman that a man loves, on that last noble page of *Henry Esmond*, "To think of her is to praise God"

NOTE —The reader must understand that what is handed from one generation to the next is merely these little packets or genes in the germ-cell and not the *completed character* such as tallness or black color Neither the tall character nor black color nor any other feature will develop unless proper environment is supplied, and if there should be a radical change in the environment it might be some other color than black would develop If either the hereditary material in the germ-cell is changed ever so slightly or the environment changed some other character develops than the one which we commonly speak of as inherited The reader must not gain the idea that these determiners will develop into some certain characteristics irrespective of the environment Professor Herbert S Jennings of The Johns Hopkins University, has brilliantly and profoundly argued this whole

matter in an article in *The Scientific Monthly* for September 1924 entitled *Heredity and Environment* As Professor Jennings puts it Clearly it is not necessary to have a characteristic merely because one inherits it. Or more properly characteristics are not inherited at all what one inherits is certain material that under certain conditions will produce a particular characteristic if those conditions are not supplied some other characteristic is produced

In this sense a man s knowledge of Latin grammar is just as much an inherited character as is his bald head Both developed because certain packets of chemicals called factors were in the germ-cell from which he was born and these factors under the conditions that he met in life developed into these characteristics Had he met different conditions he would have developed other characteristics in their stead. It is not true that a man is predetermined in or by the germ-cell and that a foreordained man with foreordained characteristics is going to grow up willy nilly However because of merely *practical difficulties* we can not very radically alter men by education and environment, partly because we do not as yet have the proper technical means and partly because the environment is fairly uniform for all human beings during the first nine months of their lives and they come into the world as quite far advanced organisms But in frogs and fruit flies and other animals where the egg itself and the early embryo can be radically interfered with changes can easily be produced which make the adult animal strikingly different from what it would have been in the usually expected environment We predict a certain kind of man by studying his ancestry merely because we *expect* for him a certain type of general environment not profoundly different from that of his ancestors It is the *expected* environment which leads us to count pretty strongly on heredity and not that the heredity in the germ package predetermines all he shall be F A Woods pointed this out nearly fifteen years ago Of course there are limits to the alterations possible by environment but they are far from being reached as yet with human beings None of this alters the fact that very moderate environmental measures such as education and moral suasion expended on rich hereditary material yield far greater results than when expended on poor material Other measures might produce as marked results with poor material but in society as a practical matter there is neither the time nor money as yet to try to make imbeciles into geniuses when by proper marriages they can be produced free of charge The differences among men are I think largely due to differences in the original hereditary packets in the germ-cells because so much of the environment of men is common to them all. I can not reproduce all of Professor Jennings fine presentation and can only urge the thoughtful to study it with care as the most penetrating discussion of the heredity-environment problem that has been made from the standpoint of a geneticist and embryologist.

CHAPTER XXXIX

EUGENICS AND EUTHENICS[1]

PAUL POPENOE AND ROSWELL H JOHNSON

Emphasis has been given, in several of the foregoing chapters, to the desirability of inheriting a good constitution and a high degree of vigor and disease resistance It has been asserted that *no measures* of hygiene and sanitation can take the place of such inheritance It is now desirable to ascertain the limits within which good inheritance is effective, and this may be conveniently done by a study of the lives of a group of people who inherited exceptionally strong physical constitutions

The people referred to are taken from a collection of histories of long life made by the Genealogical Record Office of Washington One hundred individuals were picked out at random, each of whom had died at the age of ninety or more and with the record of each individual were placed those of all his brothers and sisters Any family was rejected in which there was a record of wholly accidental death (e g , families of which a member had been killed in the Civil War) The 100 families, or more correctly fraternities or sibships, were classified by the number of children per fraternity, as follows

Number of Fraternities	Number of Children per Fraternity	Total Number of Children in Group
1	2	2
11	3	33
8	4	32
17	5	85
13	6	78
14	7	98
9	8	72
11	9	99
10	10	100
3	11	33
2	12	24
1	13	13
100		669

[1] From P Popenoe and R H Johnson *Applied Eugenics* (copyright 1918) Used by special permission of the publishers The Macmillan Company

The average at death of these 669 persons was 64 7 years The child mortality (first 4 years of life) was 7 5 per cent of the total mortality, 69 families showing no deaths of that kind The group is as a whole, therefore, long lived

The problem was to measure the resemblance between brothers and sisters in respect of longevity—to find whether knowledge of the age at which one died would justify a prediction as to the age at death of the others—or technically it was to measure the fraternal correlation of longevity A zero coefficient here would show that there is no association that from the age at which one dies nothing whatever can be predicted as to the age at which the others will die Since it is known that heredity is a large factor in longevity, such a finding would mean that all deaths were due to some accident which made the inheritance of no account.

In an ordinary population it has been found that the age at death of brothers and sisters furnishes a coefficient of correlation of the order of 3 which shows that heredity does determine the age at which one shall die to considerable extent but not absolutely [1]

The index of correlation[2] between the lengths of life within the fraternity in these 100 selected families furnished a coefficient of -0163 ± 0672 practically zero In other words if the age is known at which a member of one of these families died whether it be one month or 100 years nothing whatever can be predicted about the age at which his brothers and sisters died

[1] Mary Beeton and Karl Pearson *Biometrika* I p 60 The actual correlation varies with the age and sex the following are the results

COLLATERAL INHERITANCE

Elder adult brother and younger adult brother	2290 ± 0194
Adult brother and adult brother	2853 ± 0196
Minor brother and minor brother	1026 ± 0294
Adult brother and minor brother	− 0262 ± 0246
Elder adult sister and younger adult sister	3464 ± 0183
Adult sister and adult sister	3322 ± 0185
Minor sister and minor sister	1748 ± 0307
Adult sister and minor sister	− 0260 ± 0291
Adult brother and adult sister	2319 ± 0145
Minor brother and minor sister	1435 ± 0251
Adult brother and minor sister	− 0062 ± 0349
Adult sister and minor brother	− 0274 ± 0238

[2] The method used is the ingenious one devised by J Arthur Harris (*Biometrika* IX p 461) The probable error is based on $n = 100$

Remembering that longevity is in general inherited, and that it is found in the families of all the people of this study (since one in each fraternity lived to be 90 or over) how is one to interpret this zero coefficient? Evidently it means that although these people had inherited a high degree of longevity, their deaths were brought about by causes which prevented the heredity from getting full expression As far as hereditary potentialities are concerned, it can be said that all their deaths were due to accident, using that word in a broad sense to include all non selective deaths by disease If they had all been able to get the full benefit of their heredity, it would appear that each of these persons might have lived to 90 or more, as did the one in each family who was recorded by the Genealogical Record Office Genetically, these other deaths may be spoken of as premature

In an ordinary population, the age of death is determined to the extent of probably 50 per cent by heredity In this selected long lived population heredity appears not to be responsible in any measurable degree whatsoever for the differences in age at death

The result may be expressed in another, and perhaps more striking way Of the 669 individuals studied a hundred—namely, one child in each family—lived beyond 90, and there were a few others who did But some 550 of the group though they had inherited the potentiality of reaching the average age of 90, actually died somewhere around 60, they failed by at least one third to live up to the promise of their inheritance If we were to generalize from this single case, we would have to say that five sixths of the population does not make the most of its physical inheritance

This is certainly a fact that discourages fatalistic optimism The man who tells himself that because of his magnificent inherited constitution, he can safely take any risk is pretty sure to take too many risks and meet with a non selective—i e, genetically, a premature—death when he might in the nature of things have lived almost a generation longer

It should be remarked that most of the members of this group seem to have lived in a hard environment They appear to belong predominantly to the lower strata of society, many of them are immigrants and only a very few of them, to judge by a cursory inspection of the records possessed more than moderate means This necessitated a frugal and industrious life which in many ways was favorable to longevity but which may often have led to overexposure overwork, lack of proper medical treatment, or other causes of a non selective

death. We would not push the conclusion too far, but we can not doubt that this investigation shows the folly of ignoring the environment—shows that the best inherited constitution must have a fair chance And what has here been found for a physical character, would probably hold good in even greater degree for a mental character All that man inherits is the capacity to develop along a certain line under the influence of proper stimuli, food and exercise The object of eugenics is to see that the inherent capacity is there Given that, the educational system is next needed to furnish the stimuli The consistent eugenist is therefore an ardent euthenist He not only works for a better human stock but, because he does not want to see his efforts wasted he always works to provide the best possible environment for this better stock

In so far, then as euthenics is actually providing man with more favorable surroundings—not with ostensibly more favorable surroundings which in reality, are unfavorable—there can be no antagonism between it and eugenics Eugenics is in fact a prerequisite of euthenics for it is only the capable and altruistic man who can contribute to social progress and such a man can only be produced through eugenics

Eugenic fatalism a blind faith in the omnipotence of heredity regardless of the surroundings in which it is placed has been shown by the study of long lived families to be unjustified It was found that even those who inherited exceptional longevity usually did not live as long as their inheritance gave them the right to expect If they had had more euthenics, they should have lived longer

But this illustration certainly gives no ground for a belief that euthenics is sufficient to prolong one's life beyond the inherited limit A study of these long lived families from another point of view will reveal that heredity is the primary factor and that good environment, euthenics, is the secondary one

For this purpose we augment the 100 families of the preceding section by the addition of 240 more families like them and we examine each family history to find how many of the children died before completing the fourth year of life The data are summarized in the table on page 512

The addition of the new families (which were not subjected to any different selection than the first 100) has brought down the child mortality rate For the first 100 it was found to be 7 5 per cent. If in the above table the number of child deaths, 119 be divided by the

total number of children represented, 2,259, the child mortality rate for this population is found to be 5 27 per cent or 53 per 1,000

The smallness of this figure may be seen by comparison with the statistics of the registration area U S Census of 1880, when the child mortality (0–4 years) was 400 per thousand, as calculated by Alexander Graham Bell A mortality of 53 for the first four years of life is smaller than any district known in the United States, even to-day, can show for the *first* year of life *alone* If any city could bring the deaths of babies during their first twelve months down to 53 per 1,000, it would think it had achieved the impossible, but here is a population

CHILD MORTALITY IN FAMILIES OF LONG-LIVED STOCK, GENEALOGICAL RECORD OFFICE DATA

Size of Family	Number of Families Investigated	Number of Families Showing Deaths under Five Years	Total Number of Deaths
1 child	6	0	0
2 children	6	0	0
3	38	4	5
4	40	6	7
5	38	4	4
6	44	12	13
7	34	8	11
8	46	13	18
9	31	14	20
10	27	14	14
11	13	6	9
12	13	9	16
13	1	0	0
14	2	0	0
17	1	1	2
	340	91	119

in which 53 per 1,000 covers the deaths, not only of the fatal first 12 months, but of the following three years in addition

Now this population with an unprecedentedly low rate of child mortality is not one which had had the benefit of any Baby Saving Campaign nor even the knowledge of modern science Its mothers were mostly poor, many of them ignorant, they lived frequently under conditions of hardship, they were peasants and pioneers Their babies grew up without doctors, without pasteurized milk, without ice, without many sanitary precautions usually on rough food But they had one advantage which no amount of applied science can give after birth—namely, good heredity They had inherited exceptionally good constitutions

It is not by accident that inherited longevity in a family is associated with low mortality of its children The connection between the two facts was first discovered by Mary Beeton and Karl Pearson in their pioneer work on the inheritance of duration of life They found that high infant mortality was associated with early death of parents while the offspring of long lived parents showed few deaths in child hood The correlation of the two facts was quite regular as will be evident from a glance at the following tables prepared by A Ploetz

LENGTH OF LIFE OF MOTHERS AND CHILD MORTALITY OF THEIR DAUGHTERS (ENGLISH QUAKER FAMILIES DATA OF BEETON AND PEARSON ARRANGED BY PLOETZ)

	Year of Life in Which Mothers Died					At All Ages
	to 38	39–53	54–68	69 83	84 up	
Number of daughters	234	304	395	666	247	1 846
Number of them who died in first five years	122	114	118	131	26	511
Per cent of daughters who died	*52 1*	*37 5*	*29 9*	*19 7*	*10 5*	*27 7*

LENGTH OF LIFE OF FATHERS AND CHILD MORTALITY OF THEIR DAUGHTERS

	Year of Life in Which Fathers Died					At All Ages
	to 38	39–53	54–68	69–83	84 up	
Number of daughters	105	284	585	797	236	2 009
Number of them who died in first five years	51	98	156	177	40	522
Per cent of daughters who died	48 6	34 5	26 7	22 2	17 0	26 0

To save space we do not show the relation between parent and son it is similar to that of parent and daughter which is shown in the preceding tables In making comparison with the 340 families from the Genealogical Record Office above studied it must be noted that Dr Ploetz s tables include one year longer in the period of child mortality being computed for the first five years of life instead of the first four His percentages would therefore be somewhat lower if computed on the basis used in the American work

These various data demonstrate the existence of a considerable correlation between short life (*brachybioty* Karl Pearson calls it) in parent and short life in offspring Not only is the tendency to live long inherited but the tendency *not* to live long is likewise inherited

But perhaps the reader may think they show nothing of the sort He may fancy that the early death of a parent left the child without sufficient care, and that neglect, poverty, or some other factor of euthenics brought about the child's death Perhaps it lacked a mother's loving attention, or perhaps the father's death removed the wage-earner of the family and the child thenceforth lacked the necessities of life.

Dr Ploetz has pointed out that this objection is not valid, because the influence of the parent's death is seen to hold good even to the point where the child was too old to require any assistance If the facts applied only to cases of early death, the supposed objection might be weighty, but the correlation exists from one end of the age-scale to the other It is not credible that a child is going to be deprived of any necessary maternal care when its mother dies at the age of 69 the child herself was probably married long before the death of the mother Nor is it credible that the death of the father takes bread from the child s mouth, leaving it to starve to death in the absence of a pension for widowed mothers, if the father died at 83 when the ' child" herself was getting to be an old woman The early death of a parent may occasionally bring about the child s death for a reason wholly unconnected with heredity, but the facts just pointed out show that such cases are exceptional The steady association of the child death rate and parent death rate *at all ages* demonstrates that heredity is a common cause

But the reader may suspect another fallacy The cause of this association is really environmental, he may think, and the same poverty or squalor which causes the child to die early may cause the parent to die early They may both be of healthy, long lived stock, but forced to live in a pestiferous slum which cuts both of them off prematurely and thereby creates a spurious correlation in the statistics

We can dispose of this objection most effectively by bringing in new evidence It will probably be admitted that in the royal families *of Europe, the environment is as good as knowledge and wealth can* make it No child dies for lack of plenty of food and the best medical care even if his father or mother died young And the members of this caste are not exposed to any such unsanitary conditions or such economic pressure as could possibly cause both parent and child to die prematurely If the association between longevity of parent and child mortality holds for the royal families of Europe and their princely

relatives, it can hardly be regarded as anything but the effect of heredity—of the inheritance of a certain type of constitution

Dr Ploetz studied the deaths of 3,210 children in European royalty from this viewpoint. The following table shows the relation between father and child

LENGTH OF LIFE OF FATHERS AND CHILD MORTALITY OF THEIR CHILDREN IN ROYAL AND PRINCELY FAMILIES (PLOETZ DATA)

	Year of Life in Which Fathers Died								At All Ages
	16–25	26–35	36 45	46–55	56–65	66 75	76–85	86 up	
Number of children	23	90	367	545	725	983	444	33	3210
Number who died in first five years	12	29	115	171	200	254	105	1	88,
Per cent who died	52 2	32 2	31 3	31 4	27 6	25 8	23 6	3 0	27 6

Allowing for the smallness of some of the groups, it is evident that the amount of correlation is about the same here as among the English Quakers of the Beeton Pearson investigation whose mortality was shown in the two preceding tables In the healthiest group from the royal families—the cases in which the father lived to old age—the amount of child mortality is about the same as that of the Hyde family in America, which Alexander Graham Bell has studied—namely somewhere around 250 per 1,000 One may infer that the royal families are rather below par in soundness of constitution

All these studies agree perfectly in showing that the amount of child mortality is determined primarily by the physical constitution of the parents, as measured by their longevity In the light of these facts, the nature of the extraordinarily low child mortality shown in the 340 families from the Genealogical Record Office with which we began the study of this point, can hardly be misunderstood These families have the best inherited constitution possible and the other studies cited would make us certain of finding a low child mortality among them, even if we had not directly investigated the facts

If the interpretation which we have given is correct, the conclusion is inevitable that child mortality is primarily a problem of eugenics, and that all other factors are secondary There is found to be no warrant for the statement so often repeated in one form or another, that ' the fundamental cause of the excessive rate of infant mortality in industrial communities is poverty, inadequate incomes, and low standards of living " Royalty and its princely relatives are not

characterized by a low standard of living and yet the child mortality among them is very high—somewhere around 400 per 1 000 in cases where a parent died young If poverty is responsible in the one case it must be in the other—which is absurd Or else the logical absurdity is involved of inventing one cause to explain an effect today and a wholly different cause to explain the same effect tomorrow This is unjustifiable in any case and it is particularly so when the single cause that explains both cases is so evident If weak heredity causes high mortality in the royal families why similarly cannot weak heredity cause high infant mortality in the industrial communities? We believe it does account for much of it and that the inadequate income and low standard of living are largely the consequence of inferior heredity mental as well as physical The parents in the Genealogical Record Office files had many of them inadequate incomes and low standards of living under frontier conditions but their children grew up while those of the royal families were dying in spite of every attention that wealth could command and science could furnish

If the infant mortality problem is to be solved on the basis of knowledge and reason it must be recognized that sanitation and hygiene cannot take the place of eugenics any more than eugenics can dispense with sanitation and hygiene It must be recognized that the death rate in childhood is largely selected and that the most effective way to cut it down is to endow the children with better constitutions This cannot be done solely by any euthenic campaign it cannot be done by swatting the fly abolishing the midwife sterilizing the milk nor by any of the other panaceas sometimes proposed

But it may be objected this discussion ignores the actual facts Statistics show that infant mortality campaigns have consistently produced reductions in the death rate The figures for New York which could be matched in dozens of other cities show that the number of deaths per 1 000 births in the first year of life has steadily declined since a determined campaign to Save the Babies was started

1902	181	1909	129
1903	152	1910	125
1904	162	1911	112
1905	159	1912	105
1906	153	1913	102
1907	144	1914	95
1908	128		

To one who cannot see beyond the immediate consequences of an action, such figures as the above indeed give quite a different idea of the effects of an infant mortality campaign, than that which we have just tried to create And it is a great misfortune that euthenics so often fails to look beyond the immediate effect fails to see what may happen next year, or 10 years from now or in the next generation

We admit that it is possible to keep a lot of children alive who would otherwise have died in the first few months of life It is being done, as the New York figures, and pages of others that could be cited, prove The ultimate result is twofold

1 Some of those who are doomed by heredity to a selective death but are kept alive through the first year die in the second or third or fourth year They must die sooner or later, they have not inherited sufficient resistance to survive more than a limited time If they are by a great effort carried through the first year, it is only to die in the next This is a statement which we have nowhere observed in the propaganda of the infant mortality movement, and it is perhaps a disconcerting one It can only be proved by refined statistical methods, but several independent determinations by the English biometricians leave no doubt as to the fact This work of Karl Pearson, E C Snow, and Ethel M Elderton, was cited in our chapter on natural selection, the reader will recall how they showed that nature is weeding out the weaklings and in proportion to the stringency with which she weeds them out at the start, there are fewer weaklings left to die in succeeding years

To put the facts in the form of a truism part of the children born in any district in a given year are doomed by heredity to an early death, and if they die in one year they will not be alive to die in the succeeding year, and vice versa Of course there are in addition infant deaths which are not selective and which if prevented would leave the infant with as good chance as any to live

In the light of these researches, we are forced to conclude that baby saving campaigns accomplish less than is thought, that the supposed gain is to some extent temporary and illusory

2 There is still another consequence If the gain is by great exertions made more than temporary, if the baby who would otherwise have died in the first months is brought to adult life and reproduction, it means in many cases the dissemination of another strain of weak heredity, which natural selection would have cut off ruthlessly

in the interests of race betterment. In so far, then, as the infant mortality movement is not futile it is, from a strict biological viewpoint, often detrimental to the future of the race

Do we then discourage all attempts to save the babies? Do we leave them all to natural selection? Do we adopt the "better dead" gospel?

Unqualifiedly, no! The sacrifice of the finer human feelings, which would accompany any such course, would be a greater loss to the race than is the eugenic loss from the perpetuation of weak strains of heredity The abolition of altruistic and humanitarian sentiment for the purpose of race betterment would ultimately defeat its own end by making race betterment impossible

But race betterment will also be impossible unless a clear distinction is made between measures that really mean race betterment of a fundamental and permanent nature, and measures which do not.

We have chosen the Infant Mortality Movement for analysis in this chapter because it is an excellent example of the kind of social betterment which is taken for granted, by most of its proponents, to be a fundamental piece of race betterment, but which, as a fact, often means race impairment No matter how abundant and urgent are the reasons for continuing to reduce infant mortality wherever possible, it is dangerous to close the eyes to the fact that the gain from it is of a kind that must be paid for in other ways, that to carry on the movement without adding eugenics to it will be a short sighted policy, which increases the present happiness of the world at the cost of diminishing the happiness of posterity through the perpetuation of inferior strains

While some euthenic measures are eugenically evils, even if necessary ones, it must not be inferred that all euthenic measures are dysgenic. Many of them, such as the economic and social changes we have suggested in earlier chapters, are an important part of eugenics Every euthenic measure should be scrutinized from the evolutionary standpoint, if it is eugenic as well as euthenic, it should be wholeheartedly favored, if it is dysgenic but euthenic it should be condemned or adopted, according to whether or not the gain in all ways from its operation will exceed the damage

In general, euthenics, when not accompanied by some form of selection (i e, eugenics) ultimately defeats its own end If it is accompanied by rational selection, it can usually be indorsed. Eugenics,

on the other hand, is likewise inadequate unless accompanied by constant improvement in the surroundings, and its advocates must demand euthenics as an accompaniment of selection, in order that the opportunity for getting a fair selection may be as free as possible If the euthenist likewise takes pains not to ignore the existence of the racial factor, then the two schools are standing on the same ground, and it is merely a matter of taste or opportunity, whether one emphasizes one side or the other Each of the two factions sometimes thought to be opposing, will be seen to be getting the same end result, namely, human progress

Not only are the two schools working for the same end, but each must depend in still another way upon the other, in order to make headway The eugenist cannot see his measures put into effect except through changes in law and custom—i e , euthenic changes. He must and does appeal to euthenics to secure action The social reformer, on the other hand, cannot see any improvements made in civilization except through the discoveries and inventions of some citizens who are inherently superior in ability He in turn must depend on eugenics for every advance that is made

It may make the situation clearer to state it in the customary terms of biological philosophy Selection does not necessarily result in progressive evolution It merely brings about the adaptation of a species or a group to a given environment The tapeworm is the stock example In human evolution, the nature of this environment will determine whether adaptation to it means progress or retrogression whether it leaves a race happier and more productive, or the reverse All racial progress, or eugenics, therefore, depends on the creation of a good environment and the fitting of the race to that environment Every improvement in the environment should bring about a corresponding biological adaptation The two factors in evolution must go side by side, if the race is to progress in what the human mind considers the direction of advancement In this sense, euthenics and eugenics bear the same relation to human progress as a man's two legs do to his locomotion

Social workers in purely euthenic fields have frequently failed to remember this progress of adaptation, in their efforts to change the environment Eugenists in centering their attention on adaptation, have sometimes paid too little attention to the kind of environment to which the race was being adapted The present book holds that the

second factor is just as important as the first for racial progress that one leg is just as important as the other to a pedestrian Its only conflict with euthenics appertains to such euthenic measures as impair the adaptability of the race to the better environment they are trying to make

Some supposedly euthenic measures opposed by eugenics are not truly euthenic as for instance the limitation of a superior family in order that all may get a college education For these spurious euthenic measures something truly euthenic should be substituted

Measures which show a real conflict may be typified by the infant mortality movement There can be no doubt but that sanitation and hygiene prenatal care and intelligent treatment of mothers and babies are truly euthenic and desirable At the same time as has been shown these euthenic measures result in the survival of inferior children who directly or through their posterity will be a drag on the race Euthenic measures of this type should be accompanied by counterbalancing measures of a more eugenic character

Barring these two types euthenics forms a necessary concomitant of the eugenic program and as we have tried to emphasize eugenics is likewise necessary to the complete success of every euthenic program How foolish then is antagonism between the two forces! Both are working toward the same end of human betterment, and neither can succeed without the other When either attempts to eliminate the other from its work it ceases to advance toward its goal In which camp one works is largely a matter of taste If on a road there is a gradient to be leveled it will be brought down most quickly by two parties of workmen one cutting away at the top and the other filling in the bottom For the two parties to indulge in mutual scorn and recrimination would be no more absurd than for eugenics and euthenics to be put in opposition to each other The only reason they have been in opposition is because some of the workers did not clearly understand the nature of their work With the dissemination of a knowledge of biology this ground of antagonism will disappear

CHAPTER XL

HUMAN CONSERVATION[1]

HERBERT E. WALTER

1 HOW MANKIND MAY BE IMPROVED

There are two fundamental ways to bring about human betterment, namely, by improving the individual and by improving the race The first method consists in making the best of whatever heritage has been received by placing the individual in the most favorable environment and developing his capacities to the utmost through education The second method consists in seeking a better heritage with which to begin the life of the individual The first method is immediate and urgent for the present generation The second method is concerned with ideals for the future, and consequently does not usually present so strong an appeal to the individual

The first is the method of *euthenics*, or the science of learning to live well The second is *eugenics*, which Galton defines as ' the science of being well born

These two aspects of human betterment, however, are inseparable Any hereditary characteristic must be regarded not as an independent entity, but as *a reaction between the germplasm and its environment* The biologist who disregards the fields of educational endeavor and environmental influence, is equally at fault with the sociologist who fails sufficiently to realize the fundamental importance of the germ plasm

Without euthenic opportunity the best of heritages would never fully come to its own Without the eugenic foundation the best opportunity fails of accomplishment The euthenic point of view however, must not distract the attention now, for the present chapter is particularly concerned with the program of eugenics

2 MORE FACTS NEEDED

Since the point of attack in human heredity must be largely statistical, it is of the first importance to collect more facts Our actual knowledge is confused with a mass of tradition and opinion

[1] From H E Walter *Genetics* (copyright 1913) Used by special permission of the publishers The Macmillan Company

much of which rests upon questionable foundations The great present need is to learn more facts to sift the truth from error in what is already known and to reduce all these data to workable scientific form Much progress is being made in this direction, owing to the impetus given by the revival of Mendel s illuminating work, but as yet the science of eugenics is in its infancy

The most systematic and effective attempt in this country to collect reliable data concerning heredity in man has been initiated by the Eugenics Section of the American Breeders' Association under the secretaryship of Dr C B Davenport. In 1910 the Eugenics Record Office, with a staff of expert field and office workers and an adequate equipment of fire-proof vaults, etc., for the preservation of records was opened at Cold Spring Harbor, Long Island, New York, with Mr H H Laughlin as superintendent "The main work of this office is investigation into the laws of inheritance of traits in human beings and their application to eugenics It proffers its services free of charge to persons seeking advice as to the consequences of proposed marriage matings In a word, it is devoted to the advancement of the science and practice of eugenics" The publication of results from the Eugenics Record Office has already been begun

The Volta Bureau founded about twenty five years ago in Washington by Dr Alexander Graham Bell, is collecting data with reference to deafness and has now systematically arranged particulars concerning the history of over 20 000 individuals In England, also, the *Galton Laboratory for Eugenics, founded in 1905*, is systematically collecting facts about human pedigrees and publishing the results in a compendious "Treasury of Human Inheritance'

Besides these special bureaus of investigation, innumerable facts about the inheritance of particular traits are being incidentally brought together and made available in various institutions and asylums throughout the world which are immediately concerned with the care of defectives of different types It is in connection with such institutions for defectives that much of the most successful "field work" of the Eugenics Section of the American Breeders' Association is being accomplished in the United States.

3 FURTHER APPLICATION OF WHAT WE KNOW NECESSARY

Human performance always lags behind human knowledge Many persons who are fully aware of the right procedure do not put their knowledge into practice It follows therefore, that any pro-

gram of eugenics which does not grip the imagination of the common people in such a way as to become an effective part of their very lives is bound to remain largely an academic affair for utopians to quarrel and theorize over

It is not enough to collect facts and work out an analysis and interpretation of them for important as this preliminary step is, it must be followed by a convincing campaign of education

The lives of the unborn do not force themselves upon the average man or woman with the same insistency as the lives already begun In the midst of the overwhelming demands of the present the appeal of posterity for better blood is vague and remote If every individual regarded the germplasm he carries as a sacred trust then it would be the part of an awakened eugenic conscience to restrain that germplasm when it is known to be defective or, when it is not defective to hand it on to posterity with at least as much foresight as is exercised in breeding domestic animals and cultivated plants

The eugenic conscience is in need of development, and it is only when this becomes thoroughly aroused in the rank and file of society as well as among the leaders that a permanent and increasing better ment of mankind can be expected

4 THE RESTRICTION OF UNDESIRABLE GERMPLASM

A negative way to bring about better blood in the world is to follow the clarion call of Davenport, and dry up the streams that feed the torrent of defective and degenerate protoplasm ' This may be partially accomplished, at least in America by employing the following agencies control of immigration, more discriminating marriage laws a quickened eugenic sentiment, sexual segregation of defectives and finally, drastic measures of asexualization or steriliza tion when necessary

a) CONTROL OF IMMIGRATION

The enforcement of immigration laws tends to debar from the United States not only many undesirable individuals, but also inci dentally to keep out much potentially bad germplasm that, if admitted might play havoc with future generations

For example, during the year of 1908, 65 id ots 121 feeble-minded 184 insane, 3,741 paupers, 2,900 individuals having contagious dis eases 53 tuberculous individuals, 136 criminals and 124 prostitutes were caught in the sieve at Ellis Island alone and turned back from this country by the immigration officials. These 7 000 and more

individuals probably were the bearers of very little germplasm that we are nationally not better off without.

Eugenically, the weak point in the present application of immigration laws is that criteria for exclusion are phenotypic in nature rather than genotypic and consequently much bad germplasm comes through our gates hidden from the view of inspectors because the bearers are heterozygous, wearing a cloak of desirability over undesirable traits

It is not enough to lift the eyelid of a prospective parent of American citizens to discover whether he has some kind of an eye-disease or to count the contents of his purse to see if he can pay his own way The official ought to know if eye-disease runs in the immigrant's family and whether he comes from a race of people which, through chronic shiftlessness or lack of initiative, have always carried light purses

In selecting horses for a stock farm an expert horseman might rely to a considerable extent upon his judgment of horseflesh based upon inspection alone, but the wise breeder does more than take the chances of an ordinary horse trader He wants to be assured of the *pedigree* of his prospective stock It is to be hoped that the time will come when we, as a nation, will rise above the hazardous methods of the horse trader in selecting from the foreign applicants who knock at our portals, and that we will exercise a more fundamental discrimination than such a haphazard method affords, by demanding a knowledge of the germplasm of these candidates for citizenship, as displayed in their pedigrees

This may possibly be accomplished by having trained inspectors located abroad in the communities from which our immigrants come whose duty it shall be to look up the ancestry of prospective applicants and to stamp desirable ones with approval The national expense of such a program of genealogical inspection would be far less than the maintenance of introduced defectives, in fact it would greatly decrease the number of defectives in the country At the present time this country is spending over one hundred million dollars a year on defectives alone and each year sees this amount increased

The United States Department of Agriculture already has field agents scouring every land for desirable animals and plants to introduce into this country, as well as stringent laws to prevent the importation of dangerous weeds parasites, and organisms of various kinds Is the inspection and supervision of human blood less important?

b) MORE DISCRIMINATING MARRIAGE LAWS

Every people, including even the more primitive races, make customs or laws that tend to regulate marriage Of these the laws which relate to the eugenic aspect of marriage are the only ones that concern us in this connection ' Marriage,' says Davenport "can be looked at from many points of view In novels as the climax of human courtship, in law largely as two lines of property descent, in society, as fixing a certain status, but in eugenics which considers its biological aspect, marriage is an experiment in breeding

Certain of the United States have laws forbidding the marriage of epileptics the insane, habitual drunkards, paupers idiots, feeble minded, and those afflicted with venereal diseases It would be well if such laws were not only more uniform and widespread, but also more rigidly enforced

It is quite true that marriage laws in themselves do not necessarily control human reproduction for illegitimacy is a factor that must always be reckoned with, nevertheless such laws do have an important influence in regulating marriage and consequent reproduction

Marriage laws may however, sometimes bring about a deplorable result eugenically, as in the case of forced marriage of sexual offenders in order to legalize the offense and save the woman s honor " To compel, under the guise of legality, two defective streams of germplasm to combine repeatedly and thereby result in defective offspring just because the unfortunate event happened once illegitimately, is fundamentally a mistake Darwin says ' Except in the case of man himself hardly any one is so ignorant as to allow his worst animals to breed "

c) AN EDUCATED SENTIMENT

A far more effective means of restricting bad germplasm than placing elaborate marriage laws upon our statute books is to educate public sentiment and to foster a popular eugenic conscience, in the absence of which the safeguards of the law must forever be largely without avail

Such a sentiment already generally exists to a large extent with respect to incest, and the marriage of persons as noticeably defective as idiots or those afflicted with insanity, and also in America with respect to miscegenation but a cautious and intelligent examination of the more obscure defective traits, exhibited in the somatoplasms of the various members of families in question, is largely an ideal of the

future Under existing conditions non-eugenic considerations such as wealth social position, etc., often enter into the preliminary negotiations of a marriage alliance, but an equally unromantic caution with reference to the physical moral and mental characters that make up the biological heritage of contracting parties is less usual

The scientific attitude is not necessarily opposed to the romantic way of looking at things Science is simple "organized common sense," and romance, that dispenses with this balance-wheel, although it may be entertaining and always exciting at first, is sure to be disappointing in the end Marriages may be "made in heaven," but, as a matter of fact children are born and have to be brought up on earth It follows without saying that it will be much easier to stamp out bad germplasm when an educated sentiment becomes common among all people everywhere

d) SEGREGATION OF DEFECTIVES

Persons with hereditary defects, such as epileptics, idiots, and certain criminals, who become wards of the state, should be segregated so that their germplasm may not escape to furnish additional burdens to society "We have become so used to crime, disease and degeneracy that we take them for necessary evils That they were in the world's ignorance, is granted That they must remain so, is denied" (Davenport)

"The great horde of defectives once in the world have the right to live and enjoy as best they may whatever freedom is compatible with the lives and freedom of other members of society," says Kellicott, but society had a right to protect itself against repetitions of hereditary blunders

There is one grave danger connected with the administration of our humane and commendable philanthropies toward the unfortunate, for it frequently happens that defectives are kept in institutions until they are sexually mature or are partly self supporting, when they are liberated only to add to the burden of society by reproducing their like

Furthermore, if defectives of the same sort are collected together in the same institutions, unless sexual segregation is strictly maintained, they may by the very circumstance of proximity tend to reproduce their kind just as defectives in any isolated community tend to multiply

David Starr Jordan cites the interesting case of *cretinism* which occurs in the valley of Aosta in northern Italy, to prove the wisdom

of the sexual segregation of defectives Cretinism is an hereditary defect connected with an abnormal development of the thyroid gland which results in a peculiar form of idiocy usually associated with goitre

"In the city of Aosta the goitrous *cretin* has been for centuries an object of charity The idiot has received generous support, while the poor farmer or lal orer with brains and no goitre has had the severest of struggles In the competition of life a premium has thus been placed on imbecility and disease The *cretin* has mated with *cretin*, the goitre with goitre and charity and religion have presided over the union The result is that idiocy is multiplied and intensified The *cretin* of Aosta has been developed as a new species of man In fair weather the roads about the city are lined with these awful paupers—human beings with less intelligence than a goose, with less decency than the pig"

Whymper, writing in 1880, further observes "It is strange that self interest does not lead the natives of Aosta to place their *cretins* under such restrictions as would prevent their illicit intercourse, and it is still more surprising to find the Catholic Church actually legalizing their marriage There is something horribly grotesque in the idea of solemnizing the union of a brace of idiots, and since it is well known that the disease is hereditary and develops in successive generations the fact that such marriages are sanctioned is scandalous and infamous"

Since 1800 the *cretins* have been sexually segregated, and in 1910 Jordan reported that they were nearly all gone.

e) DRASTIC MEASURES

A fifth method of restricting undesirable germplasm in the case of confirmed criminals idiots imbeciles, and rapists may be mentioned, namely the extreme treatment of either asexualization or vasectomy The latter is a minor operation confined to the male which occupies only a few moments and requires at most only the application of a local anaesthetic such as cocaine There are no disturbing or even inconvenient after effects from this operation It consists in removing a small section of each sperm duct and is entirely effectual in preventing subsequent parenthood

In the female the corresponding operation which consists in removing a portion of each Fallopian tube, is much more severe, but not impracticable or dangerous

Eight states already have sterilization laws providing for certain cases and "could such a law be enforced in the whole United States,

less than four generations would eliminate nine tenths of the crime, insanity and sickness of the present generation in our land Asylums prisons and hospitals would decrease and the problems of the unemployed the indigent old and the hopelessly degenerate would cease to trouble civilization"

5 THE CONSERVATION OF DESIRABLE GERMPLASM

Not only negatively by the restriction of undesirable germplasm but also positively by the conservation of desirable germplasm may the eugenic ideal be approached

It is possible that if some of the philanthropic endeavor now directed toward alleviating the condition of the unfit should be directed to *enlarging the opportunity of the fit* greater good would result in the end In breeding animals and plants the most notable advances have been made by isolating and developing the best, rather than by attempting to raise the standard of mediocrity through the elimination of the worst

One leader is worth a score of followers in any community, and the science of genetics surely gives to educators the hint that it is wiser to cultivate the exceptional pupil who is often left to take care of himself than to expend all the energies of the instructor in forcing the indifferent or ordinary one up to a passing standard The campaign for human betterment in the long run must do more than *avoid mistakes* It must become aggressive and take advantage of those human mutations or combinations of traits which appear in the exceptionally endowed

There are various ways in which this improvement of society may be brought about

a) BY SUBSIDIZING THE FIT

The following unconfirmed newspaper clipping illustrates the point of what is meant by subsidizing the fit so far as certain physical characteristics are concerned 'Berlin Dec 11, 1911 The Emperor is reported to be interested in a plan proposed by Professor Otto Hauser for the propagation of a fixed German type of humanity—a type which will be as fixed as the Jewish in its characteristics if the suggestions of the professor can ever be carried out The fixed type is to be produced as follows—Only 'typical' couples are to be allowed to mate The man is to be not more than thirty years old the woman not over twenty eight and each have a perfect health certificate The man should be at least five feet seven inches tall the woman not under

five feet six inches Neither the man nor the woman should have dark hair Its tint may range from blonde to auburn The eyes of the pair should be pure blue without any tint of brown The complexion should be fair to ruddy without any suggestion of heaviness or beefiness' The nose ought to be strong and narrow the chin square and powerful and the skull well developed at the back The man and the woman must be of German descent and must bear a German name and speak the language of Germany These mated couples are to get a wedding gift of $125 and an additional grant for each child born The couples may settle in the United States if they prefer This reported attempt to establish a Prussian type of 'Hauser blondes at least points the way to one sort of a positive eugenic method that might possibly be employed with respect to certain physical characteristics

It should be remembered however, that the eugenic ideal is not by any means confined to physical traits alone

b) BY ENLARGING INDIVIDUAL OPPORTUNITY

Much good human germplasm goes to waste through ineffectiveness on account of unfavorable environment or lack of a suitable opportunity to develop

Every agency which contributes toward increasing the opportunity of the individual to attain to a better development of his latent possibilities is in harmony with a thoroughly positive eugenic practice Thus better schools, better homes better living conditions in short all euthenic endeavor directly serves the eugenic ideal by making the best out of whatever germinal equipment is present in man

c) BY PREVENTING GERMINAL WASTE

Much good protoplasm fails to find expression in the form of offspring because one or the other of possible parents is cut off either by preventable death or by social hindrances To avoid such calamities is a part of the positive program of eugenics

1 *Preventable death* —War from the eugenic point of view, is the height of folly, since presumably the brave and the physically fit march away to fight while in general the unqualified stay at home to reproduce the next generation When a soldier dies on the battlefield or in the hospital, it is not alone a brave man who is cut off, but it is the termination of a probably desirable strain of germplasm. The Thirty Years' War in Germany cost 6 000 000 lives while Napoleon in his campaigns drained the best blood of France

David Starr Jordan has presented the matter very clearly He points out that the ' man with a hoe" among the European peasantry is not the result of centuries of oppression, as he has been pictured, but rather the dull progeny resulting from generations of the unfit who were left behind when the fit went off to war never to return.

Benjamin Franklin, with characteristic wisdom, sums up the situation in the following epigram ' Wars are not paid for in war time, the bill comes later '

2 *Social hindrances* —There are many conditions of modern society which act non-eugenically

For instance, the increasing demands of professional life prolong the period necessary for preparation, which, with the "cost of high living, tends toward late marriage In this way much of the best germplasm is very often w thheld from circulation until it is too late to be effective in providing for the succeeding generation.

Certain occupations such as school teaching and nursing by women are filled by the best blood obtainable, yet this blood is denied a direct part in molding posterity, since marriage is either forbidden or regarded as a serious handicap in such lines of work Advertisements concerning "unincumbered help" and "childless apartments" tell their own deplorable tale

One of the darkest features of the dark ages from a eugenic stand point was the enforced celibacy of the priesthood, since this resulted, as a rule in withdrawing into monasteries and nunneries much of the best blood of the times, and this uneugenic custom still obtains in many quarters today

6 WHO SHALL SIT IN JUDGMENT?

In the practical application of a program of eugenics there are many difficulties, for who is qualified to sit in judgment and separate the fit from the unfit?

There are certain strongly marked characteristics in mankind which are plainly good or bad, but the principle of the independence of unit characters demonstrates that no person is wholly good or wholly bad Shall we then throw away the whole bundle of sticks because it contains a few poor or crooked ones?

The list of weakling babies for instance who were apparently physically unfit and hardly worth raising upon first judgment but who afterwards became powerful factors in the world s progress, is a notable one and includes the names of Calvin, Newton Heine Voltaire Herbert Spencer and Robert Louis Stevenson

Or, take another example Elizabeth Tuttle, the grandmother of Jonathan Edwards whose remarkable progeny was referred to in a preceding chapter, is described as a ' woman of great beauty, of tall and commanding appearance, striking carriage, of strong will, extreme intellectual vigor and mental grasp akin to rapacity " but *with an extraordinary deficiency in moral sense* She was divorced from her husband "on the ground of adultery and other immoralities The evil trait was in the blood, for one of her sisters murdered her own son and a brother murdered his own sister " That Jonathan Edwards owed his remarkable qualities largely to his grandmother rather than to his grandfather is shown by the fact that Richard Edwards, the grandfather, married again after his divorce and had five sons and one daughter, but none of their numerous progeny "rose above mediocrity, and their descendants gained no abiding reputation " As shown by subsequent events, it would have been a great eugenic mistake to have deprived the world of Elizabeth Tuttle's germplasm, although it would have been easy to find judges to condemn her.

Dr C V Chapin recently said with reference to the eugenic regulation of marriage by physician's certificate "The causes of heredity are many and very conflicting The subject is a difficult one, and I for one would hesitate to say in a great many cases where I have a pretty good knowledge of the family, where marriage would, or would not, be desirable "

Desirability and undesirability must always be regarded as relative terms more or less indefinable In attempting to define them, it makes a great difference whether the interested party holds to a puritan or a cavalier standard To show how far human judgment may err as well as how radically human opinion changes, there were in England, as recently as 1819 233 crimes punishable by death according to law

One needs only to recall the days of the Spanish Inquisition or of the Salem witchcraft persecution to realize what fearful blunders human judgment is capable of, but it is unlikely that the world will ever see another great religious inquisition, or that in applying to man the newly found laws of heredity there will ever be undertaken an equally deplorable eugenic inquisition.

It is quite apparent, finally, that although great caution and broadness of vision must be exercised in bringing about the fulfilment of the highest eugenic ideals, nevertheless in this direction lies the future path of human achievement.

CHAPTER XLI

THE PROMISE OF RACE CULTURE[1]

CALEB WILLIAMS SALEEBY

The best is yet to be

In its form of what we have called negative eugenics, the practice of our principle would assuredly reduce to an incalculable extent the amount of human defect, mental and physical, which each generation now exhibits This alone, as has been said, would be far more than sufficient to justify us A world without hereditary disease of mind and body would alone warrant the hint of Ruskin that posterity may some day look back upon us with incredulous disdain " Yet, assuming that this could be accomplished, as it will be accomplished, what more is to be hoped for? Must race culture cease merely when it has raised the average of the community by reducing to a minimum the proportion of those who are thus grossly defective in mind or body? Such disease apart are we to be content, must we be content, with the present level of mediocrity in respect of intelligence and temper and moral sentiment? Can we anticipate a London in which the present ratio of musical comedy to great opera will be reversed in which the works of Mr George Meredith will sell in hundreds of thousands whilst some of our popular novelists will have to find other means of earning a living? Can we make for a critical democracy which no political party can fool and which will choose its best to govern it? Yet more, can we undertake, now or hereafter, to provide every generation with its own Shakespeare and Beethoven and Tintoretto and Newton? What, in a word, is the promise of *positive* eugenics? It is to this aspect of the question that Mr Galton has mainly directed himself Indeed he was led to formulate the principles and ideals of the new science by his study of hereditary genius some four decades ago Let us now attempt to answer some of these questions

The production of genius —And first as to the production of genius It is this perhaps that has been the main butt of the jesters who pass for philosophers with some of us today It may be said

[1] From C W Saleeby, *Parenthood and Race Culture* (copyright 1909) Used by special permission of the publishers Moffat Yard and Company

at once that neither Mr Galton nor any other responsible person has ever asserted that we can produce genius at will The difficulties in the way of such a project—at present—are almost innumerable One or two may be cited

In the first place there is the cardinal—but by no means univer sal—difficulty that the genius is too commonly so occupied with the development and expansion of his own individuality that he has little time or energy for the purposes of the race This of course is an example of Spencer s great generalization as to the antagonism or inverse ratio between individuation and genesis

Again there is the generalization of heredity formulated by Mr Galton and named by him the *law of regression towards mediocrity* It asserts that the children of those who are above or below the mean of a race tend to return towards that mean The children of the born criminal will be probably somewhat less criminal in tendency than he though more criminal than the average citizen The children of the man of genius, if he has any will probably be nearer mediocrity than he though on the average possessing greater talent than the average citizen. It is thus not in the nature of sheer genius to reproduce on its own level. It is only the critics who are totally ignorant of the elemen tary facts of heredity that attribute to the eugenist an expectation of which no one knows the absurdity so well as he does

On the other hand it is impossible to question that the hereditary transmission of genius or great talent does occur One may cite at random such cases as that of the Bach family Thomas and Matthew Arnold James and John Stuart Mill and the reader who is inclined to believe that there is no law or likelihood in this matter must certainly make h mself acquainted with Mr Galton s *Hereditary Genius* and with such a paper as that which he printed in *Sociological Papers* 1904 furnishing an index to achievements of near kinsfolk of some of the Fellows of the Royal Society There is of course the obvious fallacy involved in the poss bility that not heredity but environment was really responsible for many of these cases It must have been a great thing to have such a father as James Mill. But it would be equally idle to imagine that the evidence can be dismissed with this criticism A Matthew Arnold a John Stuart Mill could not be manufactured out of any chance material by an ideal education continued for a thousand years.

The transmission of genius —One single instance of the trans mission of genius or great talent in a family may b• cited We shall

take the family which produced Charles Darwin, the discoverer of the fundamental principle of eugenics, and his first cousin, Francis Galton Darwin s grandfather was Erasmus Darwin, physician, poet and philosopher, and independent expounder of the doctrine of organic evolution Darwin s father was a distinguished physician, described by his son as "the wisest man I ever knew" Darwin's maternal grandfather was Josiah Wedgwood, the famous founder of the pottery works Amongst his first cousins is Mr Francis Galton He has five living sons each a man of great distinction, including Mr Francis Darwin and Sir George Darwin, both of them original thinkers honored by the presidency of the British Association No one will put such a case as this down to pure chance or to the influence of environment alone This is evidently, like many others a greatly distinguished stock The worth of such families to a nation is wholly beyond any one s powers of estimation What if Erasmus Darwin had never married!

No student of human heredity can doubt that, however limited our immediate hopes, facts such as those alluded to furnish promise of great things for the future But let us turn now from genius to what we usually call talent

The production of talent —There can be no question that amongst the promises of race-culture is the possibility of breeding such things as talent and the mental energy upon which talent so largely depends In the *Inquiries into Human Faculty* Mr Galton shows the remark able extent to which energy or the capacity for labor underlies intellectual achievement He says, of energy

' It is consistent with all the robust virtues, and makes a large practice of them possible It is the measure of fullness of life the more energy the more abundance of it, no energy at all is death, idiots are feeble and listless In the enquiries I made on the antecedents of men of science no points came out more strongly than that the leaders of scientific thought were generally gifted with remarkable energy, and that they had inherited the gift of it from their parents and grand parents It may be objected that if the race were too healthy and energetic there would be insufficient call for the exercise of the pitying and self denying virtues, and the character of men would grow harder in consequence But it does not seem reasonable to preserve sickly breeds for the sole purpose of tending them as the breed of foxes is preserved solely for sport and its attendant advantages There is little fear that misery will ever cease from the land or that the

compassionate will fail to find objects for their compassion but at present the supply vastly exceeds the demand the land is over-stocked and over-burdened with the listless and the incapable In any scheme of eugenics, energy is the most important quality to favor, it is as we have seen, the basis of living action and it is eminently transmissible by descent "

Need it be pointed out that any political system which ceases to favor or actively disfavors energy, making it as profitable to be lazy as to be active, is antieugenic, and must inevitably lead to disaster? That, however, by the way Our present point is that eugenics can reasonably promise, when its principles are recognized, to multiply the human and diminish the vegetable type in the community In so doing, it will greatly further the production of talent, and therefore of that traditional or acquired progress which men of talent and genius create Such a result will also further, though indirectly, the production of genius itself For, as Mr Galton points out, ' men of an order of ability which is now very rare, would become more frequent because the level out of which they rose would itself have risen "

This is by no means the only fashion in which an effective and practicable race culture would serve genius, and I shall not be blamed for considering this matter further by any reader who realizes, however faintly, what the man of genius is worth to the world If it were shown possible to establish such social conditions that genius could never flower in them, we should realize that their establishment would mean the putting of an end to progress and the blasting of all the highest hopes of the highest of all ages

The immediate need of this age, as of all ages, is perhaps not so much the birth of babies capable of developing into men and women of genius as the full exploitation of the possibilities of genius with which, as I fancy, every generation on the average is about as well endowed as any other There is, of course, the popular doctrine that there are no mute inglorious Miltons, that "genius will out," and that therefore if it does not appear, it is not there to appear In expressing the compelling power of genius in many cases this doctrine is not without truth Yet history abounds in instances where genius has been destroyed by environment—and we can only guess how many more instances there are of which history has no record To take the single case of musical genius, it is a lamentable thought that there may be those now living whose natural endowments, in a favorable environment, would have enabled them to write symphonies fit to place

beside Beethoven's, but whom some environmental factors—conventional, economic, educational, or what not—have silenced, or worse have persuaded to write such sterile nullities as need not here be instanced There is surely no waste in all this wasteful world so lamentable as this waste of genius.

If, then, anyone could devise for us a means by which the genius potentially existing at any time, were realized, he would have performed in effect a service equivalent to that of which eugenics repudiates the present possibility—the actual creation of genius But if we consider what the conditions are which cause the waste of genius, we realize at once that they mainly inhere in the level of the human environment of the priceless potentiality in question. As we noted elsewhere, in an age like that of Pericles genius springs up on all hands It is encouraged and welcomed because the average level of the human environment in which it finds itself is so high But if eugenics can raise the average level of intelligence, in so doing not merely does it render more likely as Mr Galton points out, the production of men of the highest ability, but it provides those conditions in which men of genius, now swamped can swim We could not undertake to produce a Shakespeare, but we might reasonably hope to produce a generation which would not destroy its Shakespeares And even if men of genius still found it necessary, as men of genius have found it necessary, to play to the gallery," they would play, as Mr Galton says of the demagogue in a eugenic age, ' to a more sensible gallery than at present.'

Darwin somewhere points out that it is not the scientific, but the unscientific man who denies future possibilities Thus though an advocate of eugenics may be applauded for his judgment if he declares that the creation of genius will forever be impossible, yet I should not care to assert that the ultimate limitations of eugenics can thus be defined We have yet to hear the last of Mendelism

Eugenics and unemployment.—Let us look now at another aspect of the promise of race-culture When the time comes that quality rather than quantity is the ideal of those who concern themselves with the population question, it is quite evident that not a few of the social problems which we now find utterly insoluble will disappear In this brief outline, we can only allude to one or two points Take, for instance, the question of unemployment. We know that some by no means small proportion of the unemployed were really destined to be unemployable from the first, as for instance by reason of hereditary

disease It were better for them and for us that they had never been born. Many more of the unemployed have been made unemployable by the influence of over-crowding, to which they were subjected in their years of development. Is there, can there be, any real and permanent remedy for overcrowding, but the erection of parenthood into an act of personal and provident responsibility?

Eugenics and woman.—Take, again, the woman question No one will deny that in many of its gravest forms, especially in its economic form, and the question of the employment of women, wisely or horribly, this depends (to a degree which few, I think realize) upon the fact that there are now (1909), for instance, 1,300,000 women in excess in this country Is it then proposed, the reader will say, by means of race-culture to exterminate the superfluous woman? Indeed, no But is the reader aware that Nature is not responsible for the existence of the superfluous woman? There are more boys than girls born in the ratio of about 103 or 104 to 100, and Nature means them all to live, boys and girls alike If they did so live, we should have merely *the problem of the superfluous man*, which would not be an economic problem at all. But we destroy hosts of all the children that are born, and since male organisms are in general less resistant than female organisms we destroy a disproportionate number of boys, so that the natural balance of the sexes is inverted Unlike ancient societies we largely practice male infanticide Can the reader believe that there is any permanent and final means of arresting this wastage of child-life, with its singular and far-reaching consequences other than the elevation of parenthood, wholly apart from the question of the selection of parents? We shall not succeed in keeping all the children alive (with a trivial number of exceptions), thereby abolishing the superfluous woman by keeping alive the boy who should have grown up to be her partner, until we greatly reduce the birth rate, as it must and will be reduced when the ideal of race-culture is realized, and no child comes into the world that is not already loved and desired in anticipation

Eugenics and cruelty to children.—This ideal, also, offers us in its realization the only complete remedy for the present ghastly cruelty under which so many children suffer even in Great Britain, even in the twentieth century Is the reader aware that the National Society for the Prevention of Cruelty to Children inquired into the ill treatment or cruel neglect of 115,000 children in the year beginning April 1st, 1906? It has been reasonably and carefully estimated that "over

half a million children are involved in the total of the wastage of child life and the torture and neglect of child life in a single year Surely Mr G R Sims to whom I would offer a hearty tribute for his recent services to childhood is justified in saying ' Against the guilt of race suicide our men of science are everywhere preaching their sermons to-day It is against the guilt of race murder that the cry of the children should ring through the land As regards race suicide and the men of science I am not so sure as to the assertion But the truth of the second sentence quoted is as indisputable as it is horrible

Now no legislation conceivable will wholly cure this evil nor avert its consequences At bottom it depends upon human nature and you can cure it only by curing the defect of human nature This in general is of course beyond the immediate powers of man but evidently we should gain the same end if only we could confine the advent of children to those parents who desired them—that is to say, those in whom human nature displayed the first if not indeed almost the only requisite for the happiness of childhood To this most beneficent and wholly moral end we shall come notwithstanding the blind and pitiable guidance of most of our accredited moral teachers today By no other means than the realization of the ideal defined that every new baby shall be loved and desired in anticipation—an ideal which is perfectly practicable—can the black stain of child murder and child torture and child neglect be removed from our civilization

Ruskin and race culture —The name of Ruskin perhaps would not occur to the reader as likely to afford support to the fair hopes of the eugenist Consider then these words from *Time and Tide*

You leave your marriages to be settled by supply and demand instead of wholesome law And thus among your youths and maidens the improvident incontinent selfish and foolish ones marry whether you will or not and beget families of children necessarily inheritors in a great degree of these parental dispositions and for whom supposing they had the best dispositions in the world you have thus provided by way of educators the foolishest fathers and mothers you could find (the only rational sentence in their letters usually is the invariable one in which they declare themselves incapable of providing for their children s education) On the other hand whosoever is wise patient unselfish and pure among your youth you keep maid or bachelor wasting their best days of natural life in painful sacrifice forbidding them their best help and best reward and carefully excluding their prudence and tenderness from any offices of

parental duty Is not this a beatific and beautifully sagacious system for a Celestial Empire, such as that of these British Isles?"

Apart from the point as to wholesome law rather than the education of opinion as the eugenic means, the foregoing passage must win the assent and respect of every eugenist. It indicates the promise of race-culture as it appeared to John Ruskin The passage has been quoted in full, not for the benefit of the ordinary thoughtful reader but for that of the professional literary man who, in this remarkable age, so far as I can judge, reads nothing but what he writes, and thus qualifies himself for dismissing Spencer or Darwin or Galton by any casual phrase

Race-culture and human variety—Now let us turn to another question Let it be asserted most emphatically that, if there is any thing in the world which eugenics or race-culture does *not* promise or desire, it is the production of a uniform type of man This delusion for which there has never been any warrant at all, possesses many of the critics of eugenics, and they have made pretty play with it, just as they do with their other delusions Let us note one or two facts which bear upon this most undesirable ideal

In the first place, it is unattainable because of the existence of what we call variation No apparatus conceivable would suffice to eliminate from every generation those who varied from the accepted type

In the second place this uniformity is supremely undesirable from the purely evolutionary point of view, because its attainment would mean the arrest of all progress All organic evolution, as we know, depends upon the struggle between creatures possessing various variations and the consequent selection of those variations which constitute their possessors best adapted or fitted to the particular environment If there is no variation there can be no evolution To aim at the suppression of variation, therefore, on supposed eugenic grounds (which would be involved in aiming at any uniform type of mankind) would be to aim at destroying the necessary condition of all racial progress The mere fact that all the critics of race-culture attribute to evolutionists of all people, the desire to suppress variation, is a pathognomonic symptom of their critical quality

And, of course, quite independently of the evolutionary function of variation—though this is cardinal and must never be forgotten by the politician of any school, since what we call individuality is variation on the human plane—the value of variation in ordinary life is wholly

incalculable It is not merely that, as Mr Galton says, "There are a vast number of conflicting ideals, of alternative characters, of incompatible civilizations, but they are wanted to give fullness and interest to life Society would be very dull if every man resembled the highly estimable Marcus Aurelius or Adam Bede" The question is not merely as to the interest of life Much more important is the fact that it takes all sorts to make a world What is the development of society but the result of the psychological division of labor in the social organism? And how could such division of labor be carried out if we had not various types of laborers? What would be the good of science if there were no poetry or music to live for? How would poetry and music help us if we had not men of science to protect our shores from plague? Obviously the existence of men of most various types is a necessity for any highly organized society Even if eugenics were capable—as it is not—of producing a complete and balanced type, fit up to a point to turn out a satisfactory poem, a satisfactory symphony or a satisfactory sofa, the utmost could not be expected of such a man in any of these directions In a word, as long as their activities are not antisocial, men cannot be of too various types. We require mystic and mathematician, poet and pathologist. Only, we want good specimens of each "The aim of eugenics," says Mr Galton, ' is to represent each class or sect by its best specimens, that done, to leave them to work out their common civilization in their own way Special aptitudes would be assessed highly by those who possessed them, as the artistic faculties by artists, fearlessness of inquiry and veracity by scientists, religious absorption by mystics, and so on. There would be self sacrificers, self tormentors, and other exceptional idealists" But at least it is better to have good rather than bad specimens of any kind, whatever that kind may be Mr Galton thinks that all except cranks would agree as to including health, energy ability, manliness, and courteous disposition amongst qualities uniformly desirable—alike in poet and pathologist. We should desire also uniformity as to the absence of the antisocial proclivities of the born criminal. So much uniformity being granted let us have with it the utmost conceivable variety—more, indeed than most of us can conceive

This point, of course, is cardinal from the point of view of practice. No progress could be made with eugenics, it would be impossible even to form a Eugenics Education Society, if each of us were to regard the particular type he belongs to as the ideal and were to seek merely

to obtain the best specimens of that type The doctrine that it takes all sorts to make a world—a doctrine very hard for youth to learn, yet unconsciously learnt by all who are capable of learning at all—must be regarded as cardinal truth for the eugenist All he asks for, all he is wise in seeking, is good specimens rather than bad Poets certainly but not poetasters, jesters certainly, but not clever fools

Time and its treasure—Taking the modern estimates of the physicists we are assured that the total period of past human existence is very brief compared with what may reasonably be predicted Granted, then, practically unlimited time, what inherent limits are there to the upward development of man as a moral and intellectual being? Shall we answer this question by a study of the nature of matter? Plainly not Shall we answer it by a study of the nature of mind? Surely not, for the study of the mind cannot inform us as to what mind might be One source of guidance alone we have, and this is the amazing contrast which exists between the mind of man at *its highest, and mind in its humblest animal forms, or shall we say* even between the highest and lowest manifestations of mind within the human species? The measureless height of the ascent thus indicated offers us no warrant for the conclusion that, as we stand on the heights of our life, our "glimpse of a height that is higher" is only a hallucination On the contrary

There is no warrant whatever for supposing that the forces which have brought us thus far are yet exhausted they have their origin in the inexhaustible Who, gazing on the earth of a hundred million years ago, could have predicted life—could have recognized, in the forces then at work and the matter in which they were displayed, the promise and potency of all terrestrial life? Who, contemplating life at a much later stage, even later mammalian, could have seen in the simian the prophecy of man? Who, examining the earliest nervous ganglia, could have foreseen the human cerebrum? The fact that we can imagine nothing higher than ourselves, that we make even our gods in our own image, offers no warrant for supposing that nothing higher will ever be What ape could have predicted man, what reptile the bird, what amoeba the bee? "There are many events in the womb of time which will be delivered" and the fairest of her sons and daughters are yet to be

But even grant, for the sake of the argument, that the intelligence *of a Newton, the musical faculty of a Bach, the moral nature of* any good mother anywhere, represent the utmost limits of which the

evolution of the psychical is capable There is every reason to deny this, but let us for the moment assume it true There still remains the thought of Wordsworth, "What one is, why may not millions be?"—a thought to which Spencer has also given utterance What is shown possible for human nature here and there, he says, is conceivable for human nature at large It is possible for a human being whilst still remaining human, to be a Shakespeare or a St. Francis, these things are thus demonstrably within the possibilities of human nature *It is therefore at the least conceivable that, in the course of* almost infinite time (even assuming, say, that intelligence must ever be limited, as even Newton's intelligence was limited)—some such capacities as his may be common property amongst men of the scientific type and so with other types We may answer Wordsworth that there is no bar thrown by Nature in the way of such a hope

What is possible—This of course is speculation and of no immediate value I would merely remind the reader that the doctrine of optimism as regards the future of mankind, which the principles of race-culture assume and which they desire to justify, was definitely shared by the great pioneers to whom we owe our understanding of those principles Notwithstanding grave nervous disorder, such as makes pessimists of most men, both Darwin and Spencer were compelled by their study of Nature to this rational optimism as regards man s future The doctrine of organic evolution and of the age long ascent of man through the selection of the fittest (who have, on the whole, been the best) for parenthood, is one not of despair but of hope Exactly half a century ago it struck horror into the minds of our predecessors Man then is only an erected ape, they thought—as if any historical doctrine however true, could shorten the dizzy distance to which man has climbed since he was simian, and man being an ape they thought his high dreams palpably vain But the measure of the accomplished hints at the measure of the possible, and the value of the historical facts lies not in themselves, *all facts* as such being as dead as are the individual atoms of the living body, but in the principles which grow out of them It is of no importance as such that man has simian ancestors it is of immeasurable importance that he should learn by what processes he has become human, and by what, indeed they became simian—which would have been a proud adjective for its own day The principles of organic progress matter for us because they are the principles of race culture the only sure means of human progress Our looking backwards does not turn us

into pillars of salt, but teaches us that the best is yet to be, and how alone it is to be attained

Elsewhere the optimistic argument of Wordsworth is quoted Here also John Ruskin

"There is as yet no ascertained limit to the nobleness of person and mind which the human creature may attain, by persevering observance of the laws of God respecting its birth and training

And Herbert Spencer

"What now characterizes the exceptionally high may be expected eventually to characterize all For that which the best human nature is capable of, is within the reach of human nature at large"

And Francis Galton

' There is nothing either in the history of domestic animals or in that of evolution to make us doubt that a race of sane men may be formed, who shall be as much superior, mentally and morally, to the modern European, as the modern European is to the lowest of the Negro races

It is earnestly to be hoped that inquiries will be increasingly directed into historical facts, with the view of estimating the possible effects of reasonable political action in the future, in gradually raising the present miserably low standard of the human race to one in which the Utopias in the dreamland of philanthropists may become practical possibilities"

Conclusion—eugenics and religion—In an early chapter it was attempted to show that eugenics is not merely moral, but is of the very heart of morality We saw that it involves taking no life, that rather it desires to make philanthrophy more philanthropic, that, at any rate so far as this eugenist is concerned, it recognizes and bows to the supreme law of love and claims to serve that law, and the ideal of social morality which is the making of human worth Eugenics may or may not be practicable, it may or may not be based upon natural truth but it is assuredly moral though I, for one would proclaim eternal war between this real morality and the damnable sham, which approves the unbridled transmission of the most hideous diseases, rotting body and soul, in the interests of good

And if religion, whatever its origin and the more questionable chapters in its past, be now "morality touched with emotion," I claim that eugenics is religious is and will ever be a religion Elsewhere I have attempted to show that religion has survived and will survive because of its survival value—its services to the life of the

societies wherein it flourishes The religion of the future, it was sought to argue, will be that which "best serves Nature's unswerving desire—fullness of life" The Founder of the Christian religion said "I am come that ye might have life, and that ye might have it more abundantly" It is higher and more abundant life that is the eugenic ideal Progress I define as the emergence and increasing dominance of mind Of progress thus conceived, man is the highest fruit hitherto He is also its appointed agent and eugenics is his instrument

To this end he must use all the powers which have blossomed in him from the dust He must claim Art and indeed in Wagner's great music drama at the moment when the prophetic Brunnhilde tells Sieglinde who has just lost her mate that she, the expectant mother, may look for the resurrection of the dead and the life of the world to come in the child Siegfried, and when the heroic theme is pronounced for the first time and followed by that which signifies redemption by love then, I think, the eugenist may thrill not merely to the music, nor the humanity of the story, but to the spiritual and scientific truth which it symbolizes

If the struggle towards individual perfection be religious, so assuredly, is the struggle, less egoistic indeed towards racial perfection If the historic meaning and purport of religion are as I conceive them and if its future evolution may thence be inferred, there can be no doubt in the prophecy that in ages to come those high aspirations and spiritual visions which astronomy has dishoused from amongst the stars, and which at their best, were ever selfish, will find a place on this human earth of ours If we have transferred our hopes from heaven to earth and from ourselves to our children, they are not less religious And they that shall be of us shall build up the old waste places, for we shall raise up the foundations of many generations

"We feel the high tradition of the world
And leave our spirits on our children's breasts"

PART V

ACCESSORY READING

CHAPTER XLII

THE RELATION OF EVOLUTION TO MATERIALISM[1]

JOSEPH LE CONTE

It is seen in the sketch given in the previous chapter that, after every struggle between theology and science, there has been a readjustment of some beliefs, a giving up of some notions which really had nothing to do with religion in a proper sense, but which had become so *associated* with religious belief as to be confounded with the latter—a giving up of some line of defense which ought never to have been held because not within the rightful domain of theology at all Until the present the whole difficulty has been the result of misconception, and Christianity has emerged from every struggle only strengthened and purified, by casting off an obstructing shell which hindered its growth But the present struggle seems to many an entirely different and far more serious matter To many it seems no longer a struggle of theology, but of essential religion itself—a deadly life and-death struggle between religion and materialism To many, both skeptics and Christians, evolution seems to be synonymous with blank materialism, and therefore cuts up by the roots every form of religion by denying the existence of God and the fact of immortality That the enemies of religion, if there be any such, should assume and insist on this identity, and thus carry over the whole accumulated evidence of evolution as a demonstration of materialism, although wholly unwarranted, is not so surprising, but what shall we say of the incredible folly of her friends in admitting the same identity!

A little reflection will explain this There can be no doubt that there is at present a strong and to many an overwhelming tendency toward materialism The amazing achievements of modern science, the absorption of intellectual energy in the investigation of external nature and the laws of matter have created a current in that direction so strong that of those who feel its influence—of those who do not stay at home, shut up in their creeds, but walk abroad in the light of modern thought—it sweeps away and bears on its bosom all

[1] From J Le Conte *Evolution* (copyright 1888) Used by special permission f the publishers D Appleton & Company

but the strongest and most reflective minds Materialism has thus become a fashion of thought, and, like all fashions, must be guarded against. This tendency has been created and is now guided by science Just at this time it is strongest in the department of biology and especially is evolution its stronghold This theory is supposed by many to be simply demonstrative of materialism. Once it was the theory of gravitation which seemed demonstrative of materialism The sustentation of the universe by law seemed to imply that Nature operates itself and needs no God. That time is passed Now it is evolution and creation by law This will also pass The theory seems to many the most materialistic of all scientific doctrines only because it is the *last* which is claimed by materialism, and the absurdity of the claim is not yet made clear to many

The truth is, there is no such necessary connection between evolution and materialism as is imagined by some There is no difference in this respect between evolution and any other law of Nature. In evolution, it is true, the last barrier is broken down, and the whole domain of Nature is now subject to law, but it is only *the last*, the march of science has been in the same direction all the time In a word evolution is not only not identical with materialism, but, to the deep thinker, it has not added a feather's weight to its probability or reasonableness Evolution is one thing and materialism quite another The one is an established law of Nature, the other an unwarranted and hasty inference from that law Let no one imagine as he is conducted by the materialistic scientist in the paths of evolution from the inorganic to the organic, from the organic to the animate from the animate to the rational and moral, until he lands as it seems to him, logically and inevitably, in universal materialism—let no such one imagine that he has walked all the way in the domain of science He has stepped across the boundary into the domain of philosophy But, on account of the strong tendency to materialism and the skilful guidance of his leaders there seems to be no such boundary, he does not distinguish between the inductions of science and the inferences of a shallow philosophy, the whole is accredited to science, and the final conclusion seems to carry with it all the certainty which belongs to scientific results The fact that these materialistic conclusions are reached by some of the foremost scientists of the present day adds nothing to their probability In a question of science, viz, the law of evolution their authority is deservedly high, but in a question of philosophy, viz,

materialism, it is far otherwise If the pure scientists smile when theological philosophers, unacquainted with the methods of science undertake to dogmatize on the subject of evolution, they must pardon the philosophers if they also smile when the pure scientists imagine that they can at once solve questions in philosophy which have agitated the human mind from the earliest times I am anxious to show the absurdity of this materialistic conclusion, but I shall try to do so, not by any labored argument, but by a few simple illustrations.

1 It is curious to observe how, when the question is concerning a work of Nature, we no sooner find out how a thing is made than we immediately exclaim ' It is not made at all, it became so of itself' So long as we knew not how worlds were made we of course concluded they must have been created, but so soon as science showed *how* it was probably done, immediately we say we were mistaken—they were not made at all So also, as long as we could not imagine how new organic forms originated, we were willing to believe they were created, but, so soon as we find that they originated by evolution, many at once say "We were mistaken no creator is necessary at all" Is this so when the question is concerning a work of man? Yes, of one kind—viz, the work of the magician Here indeed, we believe in him, and are delighted with his work, until we know how it is done, and then all our faith and wonder cease But in any honest work it is not so, but on the contrary, when we understand how it is done, stupid wonder is changed into intellectual delight Does it not seem, then that to most people God is a mere wonder worker, a chief magician? But the mission of science is to show us how things are done Is it any wonder, then, that to such persons science is constantly destroying their superstitious illusions? But if God is an honest worker, according to reason—i e, according to law—ought not science rather to change gaping wonder into intelligent delight, superstition into rational worship?

2 Again, it is curious to observe how an *old truth*, if it come only in a *new form*, often strikes us as something unheard of and even as paradoxical and almost impossible A little over thirty years ago a little philosophical toy, the gyroscope, was introduced and became

eight inches long, is set rotating rapidly, and then the free end of the

axis is supported by a string or otherwise The wheel remains suspended in the air while slowly gyrating What mysterious force sustains the wheel when its only point of support is at the end of the axle six or eight inches away? Scientific and popular literature were flooded with explanations of this seeming paradox And yet it was nothing new The boy s top, that spins and leans and will not fall, although solicited by gravity, so long as it spins, which we have seen all our lives without special wonder, is precisely the same thing

Now, evolution is no new thing, but an old familiar truth, but, coming now in a new and questionable shape, lo how it startles us out of our propriety! Origin of forms by evolution is going on everywhere about us, both in the inorganic and the organic world In its more familiar forms, it had never occurred to most of us that it was a scientific refutation of the existence of God, that it was a demonstration of materialism But now it is pushed one step farther in the direction it has always been going—it is made to include also the origin of species—only a little change in its form, and lo, how we start! To the deep thinker, now and always, there is and has been the alternative—materialism or theism God operates Nature or Nature operates itself but evolution puts no new phase on this old question For example, the origin of the individual by evolution Everybody knows that every one of us individually became what we now are by a slow process of evolution from a microscopic spherule of protoplasm and yet this did not interfere with the idea of God as our individual maker Why, then, should the discovery that the species (or first individuals of each kind) originated by evolution destroy our belief in God as the creator of species?

3 It is curious and very interesting to observe the manner in which vexed questions are always finally settled, if settled at all All vexed questions—i e, questions which have taxed the powers of the greatest minds age after age—are such only because there is a real truth on both sides Pure, unmixed error does not live to plague us long Error, when it continues to live, does so by virtue of a germ of truth contained Great questions, therefore, continue to be argued pro and con from age to age, because each side is in a sense—i e from its own point of view—true, but wrong in excluding the other point of view, and a true solution, a true rational philosophy, will always be found in a view which combines and reconciles the two partial mutually excluding views showing in what they are true and in what they are false—explaining their differences by transcending

them This is so universal and far reaching a principle that I am sure I will be pardoned for illustrating it in the homeliest and tritest fashion I will do so by means of the shield with the diverse sides, giving the story and construing it, however, in my own way There is, apparently, no limit to the amount of rich marrow of truth that may be extracted from these dry bones of popular proverbs and fables by patient turning and gnawing

We all remember, then, the famous dispute concerning the shield, with its sides of different colors, which we shall here call white and black We all remember how, after vain attempts to discover the truth by dispute, it was agreed to try the scientific method of investigation We all remember the surprising result Both parties to the dispute were right and both were wrong Each was right from his point of view, but wrong in excluding the other point of view Each was right in what he asserted, and each wrong in what he denied And the complete truth was the combination of the partial truths and the elimination of the partial errors But we must not make the mistake of supposing that truth consists in *compromise* There is an old adage that truth lies in the middle between antagonistic extremes But it seems to us that this is the place of *safety*, not of truth This is the favorite adage, therefore, of the timid man, the time-server, the fence man, not the truth seeker Suppose there had been on the occasion mentioned above one of these fence philosophers He would have said "These disputants are equally intelligent and equally valiant One side says the shield is white, the other that it is black, now truth lies in the middle, therefore, I conclude the shield is gray or neutral tint, or a sort of pepper and salt " Do we not see that he is the only man who has no truth in him? No truth is no heterogeneous mixture of opposite extremes, but a stereoscopic combination of two surface views into one solid reality

Now, the same is true of all vexed questions and I have given [illegible] trite fable again only to apply it to the case in hand

There are three possible views concerning the origin of [illegible] forms whether individual or specific. Two of these are [illegible] and mutually excluding, the third combining and reconcili[illegible] example, take the individual There are three theories [illegible] the origin of the individual The first is that of the pious [illegible]

[illegible]

Christians—i e, that we were made by a process of evolution Observe that this latter combines and reconciles the other two, and is thus the more rational and philosophical Now, there are also three exactly corresponding theories concerning the origin of species The first is that of many pious persons and many intelligent clergymen, who say that species were made at once by the Divine hand *without natural process* The second is that of the materialists, who say that species were not made at all they were derived ' they growed " The third is that of the theistic evolutionists, who think that they were created by a process of evolution—who believe that making is not inconsistent with growing The one asserts the divine agency, but denies natural process, the second asserts the natural process, but denies divine agency the third asserts *divine agency by natural process* Of the first two observe, both are right and both wrong, each view is right in what it asserts, and wrong in what it denies—each is right from its own point of view, but wrong in excluding the other point of view The third is the only true rational solution, for it includes combines and reconciles the other two, showing wherein each is right and wherein wrong It is the combination of the two partial truths, and the elimination of the partial errors But let us not fail to do perfect justice The first two views of origin, whether of the individual or of the species, are indeed both partly wrong as well as partly right but the view of the pious child and of the Christian contains by far the more essential truth Of the two sides of the shield, theirs is at least the whiter and more beautiful

But, alas! the great bar to a speedy settlement of this question and the adoption of a rational philosophy is not in the head, but in the heart—is not in the reason, but in pride of opinion, self conceit dogmatism The rarest of all gifts is a truly tolerant, rational spirit In all our gettings let us strive to get this, for *it* alone is true wisdom But we must not imagine that all the dogmatism is on one side, and that the theological Many seem to think that theology has a' *preemptive right* ' to dogmatism If so, then modern materialistic science has "*jumped the claim* " Dogmatism has its roots deep-bedded in the human heart It showed itself first in the domain of theology, because there was the seat of power In modern times it has gone over to the side of science, because here now is the place of power and fashion There are *two dogmatisms*, both equally opposed to the true rational spirit, viz, the old theological and the new scientific. The old clings fondly to old things only because they are old, the new grasps eagerly

after new things only because they are new True wisdom and true philosophy, on the contrary, tries all things both old and new, and holds fast only to that which is good and true The new dogmatism taunts the old for credulity and superstition the old reproaches the new for levity and skepticism But true wisdom perceives that they are both equally credulous and equally skeptical The old is credulous of old ideas and skeptical of new the new is skeptical of old ideas and credulous of new Both deserve the unsparing rebuke of all right minded men The appropriate rebuke for the old dogmatism has been already put in the mouth of Job in the form of a bitter sneer No doubt ye are the people and wisdom shall *die* with you' The appropriate rebuke for the new dogmatism though not put into the mouth of any ancient prophet ought to be uttered—I will under take to utter it here I would say to these modern materialists 'No doubt ye are the men, and wisdom and true philosophy were *born* with you"

Let it be observed that we are not here touching the general question of the personal agency of God in operating Nature This we shall take up hereafter All that we wish to insist on now is that the process and the law of evolution does not differ in its relation to materialism from all other processes and laws of Nature If the sustentation of the universe by the law of gravitation does not disturb our belief in God as the sustainer of the universe there is no reason why the origin of the universe by the law of evolution should disturb our faith in God as the creator of the universe If the law of gravitation be regarded as the Divine mode of sustentation, there is no reason why we should not regard the law of evolution as the Divine process of creation It is evident that if evolution be materialism, then is gravitation also materialism, then is every law of Nature and all science materialism If there be any difference at all it consists only in this that, as already said, here is the last line of defense of the supporters of supernaturalism in the realm of Nature But being the last line of defense—the last ditch—it is evident that a yielding here implies not a mere shifting of line, but a change of base, not a readjustment of details only, but a *reconstruction of Christian theology* This, I believe, is indeed necessary There can be little doubt in the mind of the thoughtful observer that we are even now on the eve of the greatest change in traditional views that has taken place since the birth of Christianity But let no one be greatly disturbed thereby For then, so now, change comes not to destroy but to fulfil all our dearest

hopes and aspirations, as then, so now, the germ of living truth has, in the course of ages, become so encrusted with meaningless traditions which stifle its growth that it is necessary to break the shell to set it free, as then, so now, it has become necessary to purge religious belief of dross in the form of trivialities and superstitions This has ever been and ever will be the function of science The essentials of religious faith it does not, it cannot, touch, but it purifies and ennobles our conceptions of Deity, and thus elevates the whole plane of religious thought.

CHAPTER XLIII

THE STATISTICAL STUDY OF VARIATION

STATISTICAL METHODS

The pioneer workers in the application of statistical methods to biological study were Sir Francis Galton and his leading disciple, Karl Pearson The use to which Galton and Pearson put their statistical methods appears later in this chapter For present purposes we may limit our study of biometry to that part of it which has to do with *variation* We have already discussed fluctuating variations, the small plus and minus differences that exist between the different members of the same species or variety This was the type of variation that Darwin considered the main raw material of evolution Examples of fluctuating variations are not far to seek Pearson cites as an illustration of fluctuating variation the number of veins in two sets of beech leaves, each set from a different tree

Number of veins	13	14	15	16	17	18	19	20	
Number of leaves									
First tree			1	4	7	9	4	1	26
Second tree	3	4	9	8	2				26
Total	3	4	10	12	9	9	4	1	

It will be noted that though there were 16 veined leaves on both trees, as well as 15- and 17 veined, the general distribution is quite different in the two trees In the first tree the most frequently occurring type is the 18 veined leaf, and the other types may be said to fluctuate about this (the "mode') In the second tree the mode is the 15 veined type and the other types fluctuate about it. It will be seen also at a glance that the types that differ most from the mode are the least frequent and that those nearest the mode are the most frequent.

Some years ago the writer had occasion to study the heredity of scale numbers in the banded region of the nine-banded armadillo As a preliminary to this study it was necessary to know the degree and

extent of variability present in the species. Consequently 508 individuals were taken at random and their scale or scute number counted. It was found that the total number of scutes in the nine bands ranged from 517 to 625 and that the commonest number was about 557. In order to get a definite idea of the distribution of the different types

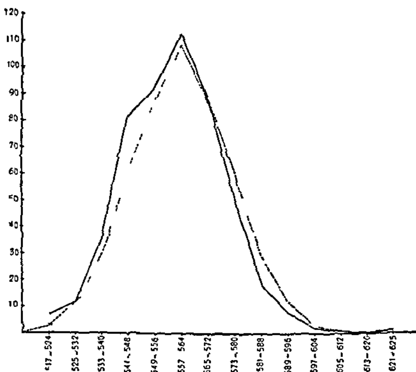


Fig. 92.—Polygon of variation for the total number of scutes in the nine bands of the armadillo (*Dasypus novemcinctus*) as determined by the seriation of 508 individuals. Class range—8 scutes. The solid line represents the observational and the broken line the theoretical normal curve. The abscissae refer to the number of scutes and the ordinates to the number of individuals. (*From Newman.*)

they were arranged in a variation polygon as shown in Figure 92. On the abscissa are arranged groups including individuals between 517 and 524 scutes inclusive, those between 525 and 532, those between 533 and 540, on up to a group of those from 621 to 625. All of these except the last included a small class with a range of 8 scutes. This arranging in classes was essential, for without it there would have been

113 classes and a very irregular and meaningless distribution On the ordinate we find by tens the numbers of individuals in each class It will be noted that the solid line is one connecting the points of inter section between the class of scute numbers and the number of individuals in these classes The dotted line represents an ideal fluctuating variation curve, which is practically a mathematical curve of chance The closeness of fit between the actual and the theoretical curve is very good The mode is the class including individuals with a scute count of 557–64, and there is a fairly even balance of individuals in the plus and the minus directions It seems fairly evident from examination of the curve that the individuals with 613 scutes and over are beyond the limits of the theoretical distribution A further study of these exceptional individuals shows that they are mutations, in which a splitting up of single scutes into paired and twinned scutes has taken place to such an extent as greatly to increase the total number of scutes

From the data used in constructing this variation polygon several significant *constants* may be obtained The ' arithmetical mean" (average number of scutes in the entire 508 individuals) is 558 2 The "median ' or halfway point between the extremes is 558 The ' mode" or most frequently occurring single type is 557 (the theoretical value being 557 6)

If we wished to compare a large group of parents with a large group of offspring, or if it were necessary to compare the armadillos of Texas with those of Mexico or Brazil, we could compare them as to mean, median, and mode, and also as to the shape of the polygon of variation This would give us a very good idea as to whether or not the old species *present in these three regions is tending to evolve in different directions* under different conditions of life

Instead of having to depend on the visual comparison between the variation polygon of two or more different populations, we can reduce the facts about the distribution of the different types about the mean or mode to a simple arithmetical constant, called the "standard deviation," which is usually given the symbol σ This constant is computed as follows

$$\sigma = \sqrt{\frac{\Sigma(x^2 f)}{n}}.$$

In this formula x represents the deviation of each class from the arithmetical mean, f, the number of individuals in each separate class Σ, the sum of all the classes, and n, the total number of individuals

By the use of this formula we have calculated the standard deviation (σ) of the individuals represented in Figure 92 to be 14 89 ± 0 31 scutes This means that the average deviation from the mean is about 14 89 scutes

The ±0 31 scutes is called the "probable error" and means that the figure 14 89 is inaccurate to the extent of being 0 31 scutes too high or too low The probable error is an essential feature of such computations as, without it, we would not be able to rely on the significance of small differences Suppose, for example, we should find that the armadillos of Brazil had a standard deviation of 15 43±0.44 scutes, we might conclude that the variability of the Brazilian individuals was 0 54 scutes greater than that of the Texas individuals In view of the fact however, that the probable error in one case is ±0 31 scutes and in the other ±0 44 scutes we would have to conclude that there was no significant difference In actual practice it has been decided that unless the actual difference between two constants is about 4 6 times as great as the probable error, the difference is not significant.

The method of determining the probable error of any calculated constant is difficult to understand, but easy to put into practice For example the formula for calculating the probable error of the standard deviation is as follows

$$E\sigma = \frac{\pm 0\ 6745\sigma}{\sqrt{2n}},$$

where E is the probable error, and n the number of individuals It will be seen that the probability of error diminishes steadily with the increase in number of individuals studied With very large numbers the error due to what is known as "random sampling" practically disappears

BIMODAL AND MULTIMODAL CURVES

If we confine our biometrical studies to homogeneous populations we get only fairly simple monomodal curves that resemble the normal curve of variation, which is a curve of chance, but when we study ordinary wild populations, we frequently find that we are dealing with a complex of several races, each of which has its own mode and standard deviation Bateson has given us a classic example of this type of phenomenon In studying the length of pinchers in the common earwig (*Forficulata auricularia*), he found that he got a two-humped or bimodal curve as shown in Figure 93 It then became evident that there were two distinct varieties as figured above Such studies have frequently revealed the heterogeneity of supposedly homogeneous

populations Opinion differs as to the significance of these findings The more optimistic evolutionists look upon such instances as that of Bateson's earwigs as visual demonstrations of a species actually splitting up into two or more species It seems quite likely that one of these types is a successful mutant type that has not fully segregated itself as a true species from the parent type Another view of the significance of bimodal curves is that the condition results from hybridization and that the bimodality is the result of the segregation of dominant and recessive types

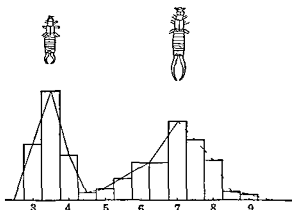


FIG 93 —Bimodal polygon plotted from data on the earwig Mean types (×½) indicated above corresponding modes Numbers below the base line indicate length of pincers in millimeters (*From Bateson and Johannsen*)

THE COEFFICIENT OF CORRELATION

Only one more biometrical constant need be mentioned here the "coefficient of correlation" It is often necessary to discover the exact relation that exists between two sets of variables in order to discover whether they are totally independent or partially correlated with each other For example, we have found that there is a close correlation between stature and head length in man, also between color of hair and color of eyes, but it is very important to be able to reduce the degree of correlation to a simple arithmetical constant This is called the "coefficient of correlation" (commonly expressed as r_{xy} where x is one variable and y the other) The formula for computing r_{xy} is as follows

$$r_{xy}=\left(\frac{\Sigma(d_xd_y)}{n}\right)\left(\frac{1}{\sigma_x\sigma_y}\right),$$

where d represents the actual deviation and Σ the sum, n the number of individuals σ the standard deviation

'Correlation tables show graphically whether or not there is correlation If, as in Figure 94, we want to find out what is the relationship between total yield of oats and number of culms to the plant, we may make a table with subject classes arranged perpendicularly, and the relative classes, horizontally If the individuals tend to group themselves about a diagonal ranging from upper left- to lower right hand corners the amount of correlation is quite marked Complete correlation would be represented by a single line of points along this diagonal No correlation would be shown by random distribution

	2	3	4	5	6	7	
0-1	3						3
1 2	28	19	3				50
2-3	18	66	20	1		1	106
3-4	1	42	58	7	1		109
4-5		7	59	11	3		80
5-6			26	14	2		42
6-7				4	3		7
7 8			1	1			2
8 9					1		1
	50	131	167	38	10	1	400

FIG 94 — Correlation table of 400 plants of Sixty Day oats Total yield of plant in grams subject Number of culms per plant relative 1910 Coefficient of correlation = 0 712 ± 0 017 (*From Love and Leighty 1914*)

over the whole rectangle Inverse correlation would tend to give a grouping about a diagonal ranging from the upper right to lower left hand corners

In the particular correlation table used for illustration, the coefficient of correlation (r_{xy}) turns out to be 0 712 ± 0 017 Since complete correlation would be 1, the degree of positive correlation is very high as we might expect The correlation table was used quite effectively by Galton as we have already shown in chapter xxxvi

CHAPTER XLIV

THE PHYSICAL BASIS OF MENDELISM[1]

ERNEST B BABCOCK AND ROY E CLAUSEN

Recent investigations in heredity have focused attention upon the chromosome mechanism as the physical basis for the segregation and recombination of the units of Mendelian inheritance The importance of cytological phenomena to students of genetics is admirably summed up by E B Wilson in the brief statement that "heredity is a consequence of the genetic continuity of cells by division, and the germ cells form the vehicle of transmission from one generation to another" It is appropriate, therefore, to introduce the subject of Mendelism with a formal and brief treatment of the chromosome mechanism and its mode of operation, on the one hand, in the building up of the body from the single cell with which the individual begins its existence, and, on the other hand, in the production of germ cells when the individual reaches the reproductive period of its life cycle It is the purpose of this chapter merely to deal with the fundamental facts of cytology which are necessary to an understanding of the connection between cell behavior and Mendelian phenomena Details unessential to such an understanding, however well established cytologically, will not be dealt with in this treatment to the end that the cardinal points may be presented as simply and as clearly as possible

The chromosomes —With few exceptions the number of chromosomes in the cells of any individual is constant and characteristic of the species to which the individual belongs Thus it is characteristic of *Drosophila ampelophila* that the cells contain eight chromosomes In maize the cells contain twenty chromosomes, in wheat sixteen, and in man forty eight, and so on through the entire plant and animal kingdoms.

Not only is the number of chromosomes in a particular species constant, but the chromosomes themselves possess a definite individuality Man and tobacco have cells with the same number of chromosomes It is needless to point out that these chromosomes,

[1] From E B Babcock and R. E Clausen, *Genetics in Relation to Agriculture* (copyright 1918) Used by special permission of the publishers The McGraw Hill Book Company

however are qualitatively very different Similarly within the species the chromosomes are not all alike on the contrary especially in certain forms they exhibit very marked differences in size and shape This is peculiarly well illustrated in *Drosophila* as shown in Fig 95 Here it is possible to recognize in the female two large pairs of curved chromosomes very similar in size and shape There is also a very small pair of chromosomes and finally there is a pair of straight ones about two-thirds as long as the large curved chromosomes In the male the same relations hold except that instead of the pair of straight chromosomes there is a pair consisting of one straight and one somewhat larger hooked chromosome The significance of this difference in chromosome content in the sexes will be pointed out in a consideration



FIG 95 —Diagram showing the characteristic pairing size relations and shapes of the chromosomes of *Drosophila melanogaster* In the male an X and a *Y* chromosome correspond to the X pair of the female On the basis of X 100 the length of each long autosome 159 of each small autosome 12 and of X 112 of the long arm of *Y* 71 and of the short arm of *Y* 41 (*From Babcock and Clausen after Bridges*)

of the inheritance of sex The pair of straight chromosomes we call the sex or X chromosomes the unequal mate of the X chromosome in the male of this species is called the Y chromosome The other chromosomes are called autosomes when it is desired to distinguish them as a class from the sex chromosomes Drosophila is not unique in possessing chromosomes of such characteristic shapes and sizes but more and more as cytology advances it is becoming possible to distinguish chromosomes and to recognize them at every cell division

Moreover the characteristic paired relations which exist among the chromosomes of Drosophila are of general significance When mature germ cells are formed in an individual reduction divisions occur by means of which the chromosome number is reduced in the germ cells to one-half that characteristic of the body cells Thus the

germ cells of Drosophila contain four chromosomes as the result of a reduction which takes place in such a manner that each germ cell contains one member of each pair of chromosomes As a consequence the germ cell of Drosophila contains two large curved autosomes representing the two pairs of these chromosomes, one small autosome and one X or one Y-chromosome The same thing is true for other species of plants and animals—in the reduction divisions the chromosomes are distributed in such a manner that each germ cell receives one member of each pair of chromosomes It follows from this that in general a definite number of *pairs* of chromosomes is characteristic of the body cells of individuals of a given species, and taking the chromosomes by pairs, one member of each pair is derived from one parent and the other from the other parent

From the standpoint of interpretation the chromosomes are aggregates of chromatin material which in itself is definitely and highly organized Our conceptions of this feature of cell organization are based on appearances of the cytological preparations from certain of the more favorable plants and animals and further interpreted by investigations on heredity Accordingly the entire chromatin content of the nucleus is regarded as made up of a definite number of individual chromatin elements called chromomeres The number of chromomeres in a cell of any species must run into the thousands A certain definite group of these elements make up each chromosome and at every cell division this chromosome is reformed from the same group of chromomeres but the chromosome is definitely organized with respect to the position or locus occupied by each chromomere At certain stages in the history of chromosomes, they are simply lines of chromomeres, very much like single strings of beads with each bead corresponding to a chromomere Now it appears probable that all the chromomeres in a chromosome are different as though our string of beads had no duplicates throughout its length Moreover, each chromomere has a definite place or locus in the particular chromosome in which it belongs and it is always found at that particular locus The chromomeres of this discussion are identified with the factors of Mendelian heredity, and how closely this conception of the nature of chromatin and its complex organization corresponds to the modern view of Mendelian phenomena will be pointed out as each new phase of Mendelism is taken up

Somatic cell division—The phenomena of cell division (called mitosis) are represented in outline in Fig 96 for a species having four

chromosomes in its body cell Bearing in mind the description which has just been given of the organization of the chromatin material we may follow the steps involved in mitosis as they are outlined in this figure In the "resting" cell at *A* the chromatin is scattered throughout the nucleus in clumps or knots loosely strung together to form an irregular network As the cell prepares for division the chromatin elements appear in more definite form until at *B* the chromomeres have

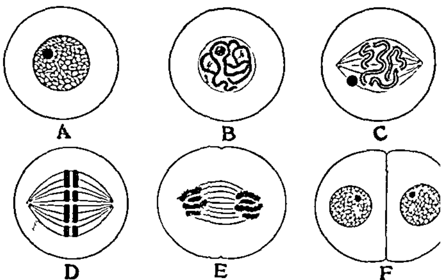


Fig 96 —Diagram of mitosis in a species having four chromosomes in its cells *A* the resting cell *B* formation of the spireme thread *C* longitudinal division of the spireme thread and transverse segmentation into four chromosomes *D* separation of the daughter chromosomes formed by longitudinal splitting of spireme thread *E* beginnings of nuclear reconstruction and division of the cell body *F* cell division complete and daughter nuclei in the resting stage (*From Babcock and Clausen*)

arranged themselves in a single row in a long continuous spireme thread This spireme-thread may be considered to be made up of the four chromosomes united end to end with the chromomeres arranged in a linear series As mitosis progresses to the next stage represented at *C*, each chromomere of the spireme thread divides into two so that a double spireme-thread results from the longitudinal splitting of the original thread Both parts of the thread are quantitatively and qualitatively equal, for, by the splitting of all the chromomeres both of the

threads come to possess all of the individual elements of the original spireme thread Following the splitting of the chromomeres and the formation of a double spireme, the spireme thread contracts and seg ments transversely forming four double chromosomes, the number characteristic of the cells of this individual This is the stage shown at *C* where also is shown the origin of the spindle, a part of the mechan ism in mitosis The chromosomes now still further contract until they assume their characteristic shapes and sizes They next appear in an equatorial position on the spindle as shown at *D*, where the two pairs of double chromosomes, one larger and one smaller, are dia grammed and the nucleolus, the large black body of the previous steps, is shown cast out and degenerating The daughter chromosomes of each pair now separate from each other until at *E* they have moved nearly to the opposite poles of the spindles and are beginning to fray out and seemingly to lose their identity At this stage actual division of the cell body has begun Finally at *F*, the chromosomes have com pletely lost all appearance of their identity, the chromatin material is distributed thruout the nucleus as in the original cell shown at *A*, and the nucleolus has been reformed in each nucleus Division of the cell body has resulted in two daughter cells each of which, so far as chromomeres are concerned, contains exactly the same chromatin elements as the original cell

There are many variations in this process particularly in the order of occurrence of the steps, but these variations in nowise modify the essential fact of mitosis which is that the chromatin material of the cell is converted into a thread which splits thruout its entire length into two halves so that the daughter nuclei receive exactly equivalent portions of chromatin material This precise division of the chromatin is brought about by a division of each chromomere so that not only do the daughter nuclei receive equivalent portions of chromatin but these portions are also equivalent qualitatively to the entire chromatin content of the mother cell By this method then each of the cells of the body finally comes to possess not only the whole num ber of chromosomes contributed by the two parents, but also the entire set of chromatin elements which it received from them. The extreme care with which the cell mechanism partitions the chromatin material in each successive cell division is in itself eloquent testimony of the fundamental importance of this material.

The production of germ cells —In the production of germ cells a different set of phenomena occur which result in a reduction of this

number of chromosomes to one half that characteristic of the somatic cells Preceding the actual reduction division the chromatin passes through a complex series of steps which may be included under the term synapsis (This term is sometimes applied in a specific sense to the pairing of homologous chromosomes and sometimes to the contraction of the chromatin threads in the conjugation stage) The essential steps in the prereduction process are shown in outline in Fig 97 At *A* is diagrammed a "resting" nucleus at the completion of

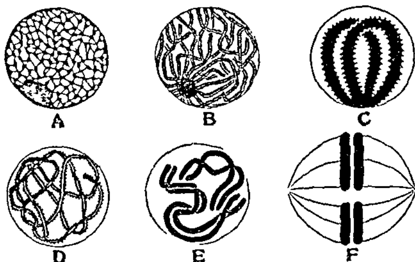


Fig 97—The reduction division as represented for a species whose diploid number is four *A*, resting nucleus of a primary germ cell, *B*, formation of paired threads of chromomeres, *C*, conjugation of homologous chromosomes (synapsis), *D* loosening of the synaptic knots *E* condensation of the chromosomes and disappearance of the nuclear membrane, *F*, homologous chromosomes about to pass to opposite poles thus giving each secondary germ cell a member of each pair and one half the somatic number (*From Babcock and Clausen*)

the multiplication divisions in the germ plasm As a result of the exact type of mitosis which has been outlined above it contains the full number of chromosomes characteristic of the species The chromatin of the nucleus next becomes organized into threads of chromomeres which pair as shown at *B* In this diagram the paired threads are taken to represent homologous chromosomes, and the opposite chromomeres of the two chromosomes The paired threads contract and

fuse along their entire length giving the figure diagrammed at C in which the two loops represent two pairs of homologous chromosomes in the conjugation stage, the essential step in synapsis Following this stage the two contracted loops of chromatin split lengthwise and unravel in somewhat the manner shown in *D* These filaments contract again forming the intertwined pairs of chromosomes shown at *E* and the nuclear membrane thereupon begins to disappear Further contraction and the formation of a spindle results in the reduction figure at *F*, the significant feature of which is the fact that each of the daughter nuclei resulting from this division receives only two chromosomes instead of the four which the original cell at *A* contained. Since the original cell contained one pair of larger and one pair of smaller chromosomes, the daughter cells which are formed each receive one larger and one smaller chromosome

Cytological investigation is not yet in agreement as to the interpretation of synapsis especially as to the manner in which the phenomena therein concerned are connected with preceding mitotic divisions Considering certain cytological investigations and the results of research in heredity together, it appears that the threads which pair in stage *B* represent pairs of chromosomes with homologous chromomeres occupying corresponding positions along their entire length Likewise the contraction stage at *C* is taken to represent a conjugation of the members of pairs of chromosomes which later again separate. Other cytological evidence indicates that in some forms the conjugation of pairs of homologous chromosomes is brought about in another way However, the essential fact is the same in either case In the reduction figure the members of each pair of chromosomes are distributed to the opposite poles of the spindle so that the daughter nuclei received only one member of each pair

The significance of synapsis lies in the conjugation of homologous chromosomes In the mitoses which have preceded this particular division, the chromosomes were each time conceived to be reformed from the identical group of chromomeres which they contained originally In synapsis however, as shown at *B* there is a certain amount of intertwining of the paired threads and in the unraveling of the chromosomes after the contraction stage there is likewise a twisting of the filaments about each other The indications are, therefore, that in synapsis there is a possibility of interchange of chromatin material between the members of a pair of homologous chromosomes In all cases however, in order to uphold our conception of the definite

organization of the chromosomes with respect to the chromomeres which they contain, this interchange of material must involve exactly equivalent portions of the two chromosomes The chromosomes of the reduction division shown at *F* may not, therefore, be identical with the four originally present in *A*, but may represent various combinations of portions of both members of a particular pair of chromosomes The results of such interchange between members of homologous pairs of chromosomes is shown in Fig 98 At the left is shown a pair of chromosomes, one in outline, the other in full black In the middle the steps in chromatin interchange are diagrammed and finally at the right this interchange results in a pair of chromosomes each of which is made up of parts of both members of the original pair of chromosomes Various combinations may result depending on the points at which interchange takes place, but in every case the exchange involves corresponding portions of the two chromosomes

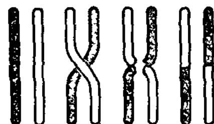


FIG 98 — Diagram of chromatin interchange between homologous members of a pair of chromosomes (*From Babcock and Clausen after Muller*)

Independent distribution of chromosomes —In Fig 99 are illustrated diagrammatically the chromosomes of Drosophila, with particular reference to their size and form relations and to their characteristic pairing in the cell One member of each of these pairs of chromosomes was contributed by the female parent and one member by the male parent In the reduction divisions these chromosomes are separated so that each germ cell contains one member of each pair of chromosomes The simplest condition which could obtain is that of independent distribution in each pair of chromosomes such that the particular member of one pair which went to a given pole of the reduction spindle would have no influence on the distribution of the members of any other pair Such independent distribution of chromosomes appears to be actually the type followed in reduction As a consequence the germ cells contain various combinations of chromosomes with respect to their original parental derivation In Fig 99 the types of combinations of maternal and paternal chromosomes and their mode of derivation in Drosophila are shown diagrammatically Two germ cells, one from the female with the chromosomes in outline,

and the other from the male with the chromosomes in full black, unite to form the female zygote shown in the middle of the figure The combinations of maternal and paternal chromosomes which result in the production of germ cells in such an individual are shown diagram

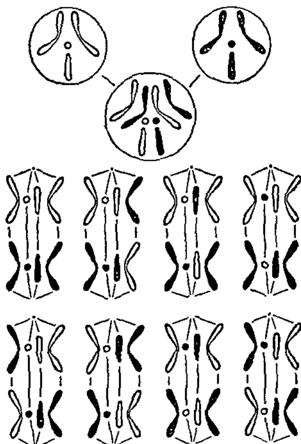


FIG 99—Diagram showing consequences of independent segregation of chromosomes in *Drosophila melanogaster* (*From Babcock and Clausen*)

matically in the lower portion of the figure There are eight different ways in which the chromosomes may be grouped in the reduction figures and on the basis of chance any one of these types is as likely to occur as any other As a result there are sixteen possible combinations of chromosomes in the germ cells with respect to the original

derivation of the chromosomes, whether from the female or from the male parent. This of course represents only the total number of possible combinations of entire chromosomes By exchange of chromatin material between homologous chromosomes resulting in the formation of combination-chromosomes the number of actual combinations is greatly increased

The number of chromosome combinations resulting from independent distribution is that number possible when each pair of chromosomes is considered separately, and every combination has an equal chance of occurrence With a form having but two pairs of chromosomes there would be only four possible combinations three pairs would give eight four pairs sixteen and in general the number of possible combinations is given by the expression 2^n in which n is the number of pairs of chromosomes in the individual in question In tobacco which has 24 pairs of chromosomes the number of possible combinations in the germ cells reaches the enormous total of 16,777,216 This means that in the formation of zygotes in a self fertilized tobacco plant the actual parental combinations, i e, combinations identical with those of the germ cells which united to form the individual in question, occur only twice in over sixteen million times, and this proportion is still further lessened when the interchange of chromatin material between homologous chromosomes is taken into account The condition of independent distribution although simple in itself results in a rapid increase in complexity with the increase in the number of pairs of chromosomes involved

Chromosomes and sex in Drosophila—The relation between inheritance and the chromosome mechanism is perhaps most simply displayed in the inheritance of sex in those animal forms in which the sexes occur in approximately equal proportions Thus in Drosophila as indicated in Fig 100 there are three pairs of autosomes which are alike in both the male and the female The remaining pair of chromosomes however, differ for the female possesses two X chromosomes whereas in the male a single X chromosome is paired with a Y chromosome and these differences are characteristic of all normal males and females of this species The bearing of these differences on the inheritance of sex is shown diagrammatically in Fig 100 Beginning with the parents the diploid number is shown in the circles representing the female and the male

In the female the three pairs of autosomes are outlined and the X chromosomes only are drawn in black to indicate that they are the ones primarily concerned in the determination of sex Similarly in

the male the three pairs of autosomes which are exactly like those in the female are outlined but the X chromosome and the Y chromosome are drawn in black The reduction division in the female results in a

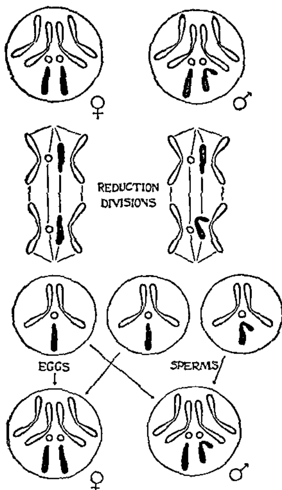


FIG 100 —Diagram showing chromosome relations in the inheritance of sex in *Drosophila melanogaster* (*From Babcock and Clausen*)

separation of the members of each pair of chromosomes so that every secondary germ cell (or egg) contains two large curved autosomes a small autosome, and an X-chromosome Consequently as far as chromosome content goes the eggs are all exactly alike In the male,

however, the separation of the members of the chromosome pairs results in sperms half of which contain an X chromosome and half a Y-chromosome in addition to the three autosomes The reduction division in the male insures an equality in numbers for the two kinds of sperm cells and the chances that either kind of sperm will fertilize an egg cell are equal By this arrangement the numerical equality of the sexes is maintained When, later, the egg cells of the female are fertilized by the sperm cells of the male, as shown in the lower portion of the figure, half of them being fertilized by sperm cells which contain an X chromosome will give females, and half uniting with sperm cells which contain Y chromosomes will produce males The inheritance of sex in Drosophila provides a beautiful illustration of the parallel behavior of the chromosome mechanism and a somatic difference, in this case sex

To recapitulate the essential phenomena of cell behavior which furnish the mechanism for the distribution of hereditary factors are these

1 Every species is characterized by a definitely organized group of chromosomes The chromosomes occur in pairs, in each of which one member is derived from each parent In ordinary somatic mitosis the distribution of chromatin is such that each daughter cell receives a full complement of chromosomes which are equivalent qualitatively to those of the mother cell

2 In germ cell formation the homologous chromosomes conjugate during synapsis, then separate, and pass into a division figure in which entire homologous chromosomes are opposed to each other The resulting reduction division gives daughter cells with half the number of chromosomes characteristic of the species the half number being made up of one member of each pair of chromosomes During synapsis there is an opportunity for the members of a pair of chromosomes to exchange chromatin material When such interchange takes place equivalent portions of chromosomes both qualitatively and quantitatively are involved In the reduction division segregation within one pair of chromosomes is entirely independent of that of any other pair so that the combinations of parental chromosomes in the germ cells represent all those to be expected on the basis of chance distribution

The student should constantly endeavor to harmonize this conception of the distributing mechanism of the chromatin material with the Mendelian interpretations of hereditary phemomena which will be presented in what follows, to the end that he may obtain a clear and definite idea of the interrelations between the known facts of heredity and cell behavior

CHAPTER XLV

NATURAL SELECTION

CHARLES DARWIN

INTRODUCTORY NOTE —This entire chapter is made up of carefully chosen passages from Darwin s *Origin of Species* So much has falsely been called ' Darwinism" that it is well for the reader to have a statement of Darwin's views in his own words Every student of evolution should read the whole of the *Origin* [illegible] polated, and then follow examples of the way in which adaptations are accounted for by natural selection Darwin s own statement of the most serious difficulties and objections to the theory, and his answers to these bring this chapter to a close

FOUNDATION STONES OF NATURAL SELECTION

DARWIN S OWN ESTIMATE AS TO THE RÔLE OF NATURAL SELECTION IN EVOLUTION

No one ought to feel surprised at much remaining as yet unexplained in regard to the origin of species and varieties, if he make due allowance for our profound ignorance in regard to the mutual relations of the many beings which live around us Who can explain why one species ranges widely and is very numerous, and why another allied species has a narrow range and is rare? Yet these relations are of the highest importance, for they determine the present welfare and, as I believe, the future success and modification of every inhabitant of this world Still less do we know of the mutual relations of the innumerable inhabitants of the world during the many past geological epochs in its history Although much remains obscure, and will long remain obscure I can entertain no doubt, after the most deliberate study and dispassionate judgment of which I am capable, that the view which most naturalists until recently entertained, and which I formerly entertained—namely, that each species has been independently created—is erroneous I am fully convinced that species are not immutable, but that those belonging to what are called the same genera are lineal descendants of some other and generally extinct species, in the same manner as the acknowledged varieties of any one species are the descendants of that species Furthermore, I am convinced that Natural Selection has been the most important, but not the exclusive, means of modification

EFFECTS OF HABIT AND OF THE USE OR DISUSE OF PARTS CORRELATED VARIATION INHERITANCE

Changed habits produce an inherited effect as in the period of the flowering of plants when transported from one climate to another With animals the increased use or disuse of parts has had a more marked influence thus I find in the domestic duck that the bones of the wing weigh less and the bones of the leg more in proportion to the whole skeleton than do the same bones in the wild-duck and this change may be safely attributed to the domestic duck flying much less and walking more than its wild parents The great and inherited development of the udders in cows and goats in countries where they are habitually milked in comparison with these organs in other countries is probably another instance of the effects of use. Not one of our domestic animals can be named which has not in some country drooping ears and the view, which has been suggested that the drooping is due to disuse of the muscles of the ear, from the animals being seldom much alarmed seems probable

Many laws regulate variation some few of which can be dimly seen and will hereafter be briefly discussed I will here only allude to what may be called correlated variation Important changes in the embryo or larva will probably entail changes in the mature animal In monstrosities the correlations between quite distinct parts are very curious and many instances are given in Isidore Geoffroy St Hilaire s great work on this subject Breeders believe that long limbs are almost always accompanied by an elongated head Some instances of correlation are quite whimsical thus cats which are entirely white and have blue eyes are generally deaf but it has been lately stated by Mr Tait that this is confined to the males Color and constitutional peculiarities go together of which many remarkable cases could be given amongst animals and plants From facts collected by Heusinger it appears that white sheep and pigs are injured by certain plants whilst dark colored individuals escape Professor Wyman has recently communicated to me a good illustration of this fact on asking some farmers in Virginia how it was that all their pigs were black they informed him that the pigs ate the paint root (Lachnanthes) which colored their bones pink and which caused the hoofs of all but the black varieties to drop off and one of the crackers (i e Virginia squatters) added we select the black members of a litter for raising as they alone have a good chance of living Hairless dogs have imperfect teeth long haired and coarse-haired animals are apt to

have, as is asserted, long or many horns, pigeons with feathered feet have skin between their outer toes, pigeons with short beaks have small feet, and those with long beaks large feet Hence if man goes on selecting, and thus augmenting, any peculiarity, he will almost certainly modify unintentionally other parts of the structure, owing to the mysterious laws of correlation

DARWIN S IDEA OF THE CAUSES RESPONSIBLE FOR THE ORIGIN OF DOMESTIC RACES

To sum up on the origin of our domestic races of animals and plants Changed conditions of life are of the highest importance in causing variability, both by acting directly on the organization, and indirectly by affecting the reproductive system It is not probable that variability is an inherent and necessary contingent, under all circumstances The greater or less force of inheritance and reversion determine whether variations shall endure Variability is governed by many unknown laws, of which correlated growth is probably the most important Something but how much we do not know, may be attributed to the definite action of the conditions of life Some, perhaps a great, effect may be attributed to the increased use or disuse of parts The final result is thus rendered infinitely complex In some cases the intercrossing of aboriginally distinct species appears to have played an important part in the origin of our breeds When several breeds have once been formed in any country, their occasional intercrossing, with the aid of selection, has, no doubt, largely aided in the formation of new sub breeds, but the importance of crossing has been much exaggerated, both in regard to animals and to those plants which are propagated by seed With plants which are temporarily propagated by cuttings, buds, etc, the importance of crossing is immense, for the cultivator may here disregard the extreme variability both of hybrids and of mongrels, and the sterility of hybrids, but plants not propagated by seed are of little importance to us, for their endurance is only temporary Over all these causes of Change, the accumulative action of Selection, whether applied methodically and quickly, or unconsciously and slowly but more efficiently, seems to have been the predominant Power

DARWIN S IDEA OF THE ORIGIN OF VARIETIES SPECIES AND GENERA IN NATURE

Finally, varieties cannot be distinguished from species—except, first, by the discovery of intermediate linking forms, and, secondly, by a certain indefinite amount of difference between them, for two

forms if differing very little, are generally ranked as varieties notwithstanding that they cannot be closely connected, but the amount of difference considered necessary to give to any two forms the rank of species cannot be defined In genera having more than the average number of species in any country, the species of these genera have more than the average number of varieties In large genera the species are apt to be closely but unequally, allied together, forming little clusters round other species Species very closely allied to other species apparently have restricted ranges In all these respects the species of large genera present a strong analogy with varieties And we can clearly understand these analogies, if species once existed as varieties and thus originated whereas, these analogies are utterly inexplicable if species are independent creations

We have also seen that it is the most flourishing or dominant species of the larger genera within each class which on an average yield the greatest number of varieties, and varieties, as we shall hereafter see tend to become converted into new and distinct species Thus the larger genera tend to become larger, and throughout nature the forms of life which are now dominant tend to become still more dominant by leaving many modified and dominant descendants But by steps hereafter to be explained the larger genera also tend to break up into smaller genera And thus, the forms of life throughout the universe become divided into groups subordinate to groups

THE TERM STRUGGLE FOR EXISTENCE USED IN A LARGE SENSE

I should premise that I use this term in a large and metaphorical sense including dependence of one being on another and including (which is more important) not only the life of the individual but success in leaving progeny Two canine animals in a time of dearth may be truly said to struggle with each other which shall get food and live But a plant on the edge of a desert is said to struggle for life against the drought though more properly it should be said to be dependent on the moisture A plant which annually produces a thousand seeds of which only one of an average comes to maturity may be more truly said to struggle with the plants of the same and other kinds which already clothe the ground The mistletoe is dependent on the apple and a few other trees but can only in a far fetched sense be said to struggle with these trees for if too many of these parasites grow on the same tree it languishes and dies But several seedling mistletoes growing close together on the same branch

sions and they are almost necessary for brevity So again it is difficult to avoid personifying the word Nature but I mean by Nature only the aggregate action and product of many natural laws and by laws the sequence of events as ascertained by us With a little familiarity such superficial objections will be forgotten

We shall best understand the probable course of natural selection by taking the case of a country undergoing some slight physical change for instance of climate The proportional numbers of its inhabitants will almost immediately undergo a change and some species will probably become extinct We may conclude from what we have seen of the intimate and complex manner in which the inhabitants of each country are bound together that any change in the numerical proportions of the inhabitants independently of the change of climate itself would seriously affect the others If the country were open on its borders new forms would certainly immigrate and this would likewise seriously disturb the relations of some of the former inhabitants Let it be remembered how powerful the influence of a single introduced tree or mammal has been shown to be But in the case of an island or of a country partly surrounded by barriers into which new and better adapted forms could not freely enter we should then have places in the economy of nature which would assuredly be better filled up if some of the original inhabitants were in some manner modified for had the area been open to immigration these same places would have been seized on by intruders In such cases slight modifications which in any way favored the individuals of any species by better adapting them to their altered conditions would tend to be preserved and natural selection would have free scope for the work of improvement.

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We have good reason to believe, as shown in the first chapter, that changes in the conditions of life give a tendency to increased variability and in the foregoing cases the conditions have changed, and this would manifestly be favorable to natural selection by affording a better chance of the occurrence of profitable variations Unless such occur, natural selection can do nothing Under the term of "variations," it must never be forgotten that mere individual differences are included As man can produce a great result with his domestic animals and plants by adding up in any given direction individual differences, so could natural selection, but far more easily from having incomparably longer time for action Nor do I believe that any great physical change, as of climate, or any unusual degree of isolation to check immigration,

is necessary in order that new and unoccupied places should be left, for natural selection to fill up by improving some of the varying inhabitants For as all the inhabitants of each country are struggling together with nicely balanced forces, extremely slight modifications in the structure or habits of one species would often give it an advantage over others, and still further modifications of the same kind would often still further increase the advantage, as long as the species continued under the same conditions of life and profited by similar means of subsistence and defense No country can be named in which all the native inhabitants are now so perfectly adapted to each other and to the physical conditions under which they live, that none of them could be still better adapted or improved, for in all countries, the natives have been so far conquered by naturalized productions, that they have allowed some foreigners to take firm possession of the land And as foreigners have thus in every country beaten some of the natives, we may safely conclude that the natives might have been modified with advantage so as to have better resisted the intruders

As man can produce and certainly has produced, a great result by his methodical and unconscious means of selection, what may not natural selection effect? Man can act only on external and visible characters Nature, if I may be allowed to personify the natural preservation or survival of the fittest, cares nothing for appearances except in so far as they are useful to any being She can act on every internal organ, on every shade of constitutional difference, on the whole machinery of life Man selects only for his own good Nature only for that of the being which she tends Every selected character is fully exercised by her, as is implied by the fact of their selection Man keeps the natives of many climates in the same country, he seldom exercises each selected character in some peculiar and fitting manner, he feeds a long and a short beaked pigeon on the same food he does not exercise a long backed or long legged quadruped in any peculiar manner, he exposes sheep with long and short wool to the same climate He does not allow the most vigorous males to struggle for the females He does not rigidly destroy all inferior animals, but protects during each varying season, as far as lies in his power, all his productions He often begins his selection by some half monstrous form or at least by some modification prominent enough to catch the eye or to be plainly useful to him Under nature, the slightest differences of structure or constitution may well turn the nicely balanced scale in the struggle for life and so be preserved How fleeting are the

wishes and efforts of man! how short his time! and consequently how poor will be his results, compared with those accumulated by Nature during whole geological periods! Can we wonder then, that Nature's productions should be far' truer in character than man's productions that they should be infinitely better adapted to the most complex conditions of life, and should plainly bear the stamp of far higher workmanship?

It may metaphorically be said that natural selection is daily and hourly scrutinizing, throughout the world the slightest variations rejecting those that are bad, preserving and adding up all that are good, silently and insensibly working whenever and wherever oppor tunity offers, at the improvement of each organic being in relation to its organic and inorganic conditions of life We see nothing of these slow changes in progress until the hand of time has marked the lapse of ages, and then so imperfect is our view into long past geological ages, that we see only that the forms of life are now different from what they formerly were

In order that any great amount of modification should be effected in a species a variety when once formed must again perhaps after a long interval of time, vary or present individual differences of the same favorable nature as before and these must be again preserved, and so onwards step by step Seeing that individual differences of the same kind perpetually recur, this can hardly be considered as an unwarrantable assumption But whether it is true, we can judge only by seeing how far the hypothesis accords with and explains the general phenomena of nature On the other hand, the ordinary belief that the amount of possible variation is a strictly limited quantity is likewise a simple assumption

Although natural selection can act only through and for the good of each being yet characters and structures, which we are apt to con sider as of very trifling importance, may thus be acted on When we see leaf-eating insects green and bark feeders mottled gray, the alpine ptarmigan white in winter, the red grouse the color of heather, we must believe that these tints are of service to these birds and insects in preserving them from danger Grouse, if not destroyed at some period of their lives would increase in countless numbers, they are known to suffer largely from birds of prey, and hawks are guided by eyesight to their prey—so much so, that on parts of the Continent persons are warned not to keep white pigeons, as being the most liable to destruction Hence natural selection might be effective in giving

the proper color to each kind of grouse, and in keeping that color, when once acquired true and constant Nor ought we to think that the occasional destruction of an animal of any particular color would produce little effect we should remember how essential it is in a flock of white sheep to destroy a lamb with the faintest trace of black. We have seen how the color of the hogs, which feed on the ' pa nt root ' in Virginia determines whether they shall live or die In plants, the down on the fruit and the color of the flesh are considered by botanists as characters of the most trifling importance yet we hear from an excellent horticulturist, Downing, that in the United States smooth skinned fruits suffer far more from a beetle, a Curculio than those with down that purple plums suffer far more from a certain disease than yellow plums whereas another disease attacks yellow fleshed peaches far more than those with other colored flesh If, with all the aids of art, these slight differences make a great difference in cultivating the several varieties, assuredly, in a state of nature, where the trees would have to struggle with other trees and with a host of enemies, such differences would effectually settle which variety, whether a smooth or downy, a yellow or purple-fleshed fruit, should succeed

In looking at many small points of difference between species which, as far as our ignorance permits us to judge, seem quite unimportant, we must not forget that climate, food, etc., have no doubt produced some direct effect. It is also necessary to bear in mind that owing to the law of correlation when one part varies, and the variations are accumulated through natural selection, other modifications often of the most unexpected nature will ensue

As we see that those variations which under domestication appear at any particular period of life tend to reappear in the offspring at the same period, for instance, in the shape size, and flavor of the seeds of the many varieties of our culinary and agricultural plants, in the caterpillar and cocoon stages of the varieties of the silk worm, in the eggs of poultry, and in the color of the down of their chickens, in the horns of our sheep and cattle when nearly adult, so in a state of nature natural selection will be enabled to act on and modify organic beings at any age by the accumulation of variations profitable at that age and by their inheritance at a corresponding age If it profit a plant to have its seeds more and more widely disseminated by the wind I can see no greater difficulty in this being effected through natural selection, than in the cotton planter increasing and improving by selection the down in the pods on his cotton trees Natural

selection may modify and adapt the larva of an insect to a score of contingencies wholly different from those which concern the mature insect, and these modifications may affect through correlation the structure of the adult So conversely, modifications in the adult may affect the structure of the larva, but in all cases natural selection will ensure that they shall not be injurious for if they were so the species would become extinct

Natural selection will modify the structure of the young in relation to the parent and of the parent in relation to the young In social animals it will adapt the structure of each individual for the benefit of the whole community, if the community profits by the selected change What natural selection cannot do is to modify the structure of one species without giving it any advantage for the good of another species, and though statements to this effect may be found in works of natural history I cannot find one case which will bear investigation A structure used only once in an animal s life if of high importance to it might be modified to any extent by natural selection for instance the great jaws possessed by certain insects used exclusively for opening the cocoon—or the hard tip to the beak of unhatched birds, used for breaking the egg It has been asserted that of the best short beaked tumbler pigeons a greater number perish in the egg than are able to get out of it so that fanciers assist in the act of hatching Now if nature had to make the beak of a full grown pigeon very short for the bird s own advantage the process of modification would be very slow, and there would be simultaneously the most rigorous selection of all the young birds within the egg which had the most powerful and hardest beaks for all with weak beaks would inevitably perish, or, more delicate and more easily broken sh lls might be selected the thickness of the shell being known to vary like every other structure

It may be well here to remark that with all beings there must be much fortuitous destruction which can have little or no influence on the course of natural selection For instance a vast number of eggs or seeds are annually devoured and these could be modified through natural selection only if they varied in some manner which protected them from their enemies Yet many of these eggs or seeds would perhaps if not destroyed have yielded individuals better adapted to their conditions of life than any of those which happened to survive So again a vast number of mature animals and plants, whether or not they be the best adapted to their conditions must be annually

destroyed by accidental causes which would not be in the least degree mitigated by certain changes of structure or constitution which would in other ways be beneficial to the species But let the destruction of the adults be ever so heavy, if the number which can exist in any district be not wholly kept down by such causes, or again let the destruction of eggs or seeds be so great that only a hundredth or a thousandth part are developed, yet of those which do survive, the best adapted individuals, supposing that there is any variability in a favorable direction, will tend to propagate their kind in larger numbers than the less well adapted If the numbers be wholly kept down by the causes just indicated, as will often have been the case, natural selection will be powerless in certain beneficial directions, but this is no valid objection to its efficiency at other times and in other ways for we are far from having any reason to suppose that many species ever undergo modification and improvement at the same time in the same area

SEXUAL SELECTION

Inasmuch as peculiarities often appear under domestication in one sex and become hereditarily attached to that sex, so no doubt it will be under nature Thus it is rendered possible for the two sexes to be modified through natural selection in relation to different habits of life, as is sometimes the case, or for one sex to be modified in relation to the other sex, as commonly occurs This leads me to say a few words on what I have called Sexual Selection This form of selection depends, not on a struggle for existence in relation to other organic beings or to external conditions, but on a struggle between the individuals of one sex, generally the males, for the possession of the other sex The result is not death to the unsuccessful competitor, but few or no offspring Sexual selection is, therefore, less rigorous than natural selection Generally, the most vigorous males, those which are best fitted for their places in nature, will leave most progeny But in many cases, victory depends not so much on general vigor, as on having special weapons, confined to the male sex. A hornless stag or spurless cock would have a poor chance of leaving numerous offspring Sexual selection, by always allowing the victor to breed, might surely give indomitable courage length to the spur, and strength to the wing to strike in the spurred leg in nearly the same manner as does the brutal cock fighter by the careful selection of his best cocks How low in the scale of nature the law of battle descends, I know not, male alligators have been described as fighting, bellowing, and whirl

ing around, like Indians in a war-dance, for the possession of the females, male salmons have been observed fighting all day long, male stag beetles sometimes bear wounds from the huge mandibles of other males, the males of certain hymenopterous insects have been frequently seen by that inimitable observer M Fabre, fighting for a particular female who sits by, an apparently unconcerned beholder of the struggle, and then retires with the conqueror The war is perhaps, severest between the males of polygamous animals, and these seem oftenest provided with special weapons The males of carnivorous animals are already well armed, though to them and to others, special means of defense may be given through means of sexual selection, as the mane of the lion, and the hooked jaw to the male salmon, for the shield may be as important for victory as the sword or spear

Amongst birds, the contest is often of a more peaceful character All those who have attended to the subject believe that there is the severest rivalry between the males of many species to attract, by singing, the females The rock-thrush of Guiana, birds of paradise, and some others, congregate, and successive males display with the most elaborate care, and show off in the best manner, their gorgeous plumage, they likewise perform strange antics before the females, which, standing by as spectators, at last choose the most attractive partner Those who have closely attended to birds in confinement well know that they often take individual preferences and dislikes thus Sir R Heron has described how a pied peacock was eminently attractive to all his hen birds I cannot here enter on the necessary details, but if man can in a short time give beauty and an elegant carriage to his bantams, according to his standard of beauty, I can see no good reason to doubt that female birds by selecting, during thousands of generations, the most melodious or beautiful males, according to their standard of beauty, might produce a marked effect Some well known laws, with respect to the plumage of male and female birds, in comparison with the plumage of the young, can partly be explained through the action of sexual selection on variations occurring at different ages, and transmitted to the males alone or to both sexes at corresponding ages, but I have not space here to enter on this subject

Thus it is, as I believe, that when the males and females of any animal have the same general habits of life, but differ in structure, color, or ornament such differences have been mainly caused by sexual

selection that is, by individual males having had, in successive generations, some slight advantage over other males, in their weapons means of defence, or charms, which they have transmitted to their male offspring alone Yet, I would not wish to attribute all sexual differences to this agency for we see in our domestic animals peculiarities arising and becoming attached to the male sex, which apparently have not been augmented through selection by man The tuft of hair on the breast of the wild turkey cock cannot be of any use, and it is doubtful whether it can be ornamental in the eyes of the female bird, indeed, had the tuft appeared under domestication, it would have been called a monstrosity

ILLUSTRATIONS OF THE ACTION OF NATURAL SELECTION, OR THE SURVIVAL OF THE FITTEST

In order to make it clear how, as I believe, natural selection acts, I must beg permission to give one or two imaginary illustrations Let us take the case of a wolf, which preys on various animals, securing some by craft, some by strength, and some by fleetness, and let us suppose that the fleetest prey, a deer for instance, had from any change in the country increased in numbers, or that other prey had decreased in numbers, during that season of the year when the wolf was hardest pressed for food Under such circumstances the swiftest and slimmest wolves would have the best chance of surviving and so be preserved or selected, provided always that they retained strength to master their prey at this or some other period of the year, when they were compelled to prey on other animals I can see no more reason to doubt that this would be the result, than that man should be able to improve the fleetness of his greyhounds by careful and methodical selection, or by that kind of unconscious selection which follows from each man trying to keep the best dogs without any thought of modifying the breed I may add, that, according to Mr Pierce, there are two varieties of the wolf inhabiting the Catskill Mountains, in the United States, one with a light greyhound like form, which pursues deer, and the other more bulky, with shorter legs, which more frequently attacks the shepherd's flocks

It should be observed that, in the above illustration, I speak of the slimmest individual wolves, and not of any single strongly marked variation having been preserved In former editions of this work I sometimes spoke as if this latter alternative had frequently occurred I saw the great importance of individual differences, and this led me fully to discuss the results of unconscious selection by man which

depends on the preservation of all the more or less valuable individuals, and on the destruction of the worst I saw, also, that the preservation in a state of nature of any occasional deviation of structure, such as a monstrosity, would be a rare event, and that, if at first preserved, it would generally be lost by subsequent intercrossing with ordinary individuals Nevertheless, until reading an able and valuable article in the *North British Review* (1867), I did not appreciate how rarely single variations, whether slight or strongly marked, could be perpetuated The author takes the case of a pair of animals, producing during their lifetime two hundred offspring, of which, from various causes of destruction, only two on an average survive to pro create their kind This is rather an extreme estimate for most of the higher animals, but by no means so for many of the lower organisms He then shows that if a single individual were born, which varied in some manner, giving it twice as good a chance of life as that of the other individuals, yet the chances would be strongly against its survival Supposing it to survive and to breed, and that half its young inherited the favorable variation, still, as the Reviewer goes on to show, the young would have only a slightly better chance of surviving and breeding, and this chance would go on decreasing in the succeeding generations The justice of these remarks cannot, I think, be disputed If, for instance, a bird of some kind could procure its food more easily by having its beak curved, and if one were born with its beak strongly curved, and which consequently flourished, nevertheless there would be a very poor chance of this one individual perpetuating its kind to the exclusion of the common form, but there can hardly be a doubt, judging by what we see taking place under domestication, that this result would follow from the preservation during many generations of a large number of individuals with more or less strongly curved beaks, and from the destruction of a still larger number with the straightest beaks

SUMMARY OF CHAPTER ON NATURAL SELECTION

If under changing conditions of life organic beings present individual differences in almost every part of their structure, and this cannot be disputed, if there be, owing to their geometrical rate of increase, a severe struggle for life at some age season, or year, and this certainly cannot be disputed, then, considering the infinite complexity of the relations of all organic beings to each other and to their conditions of life, causing an infinite diversity in structure, constitution, and habits, to be advantageous to them, it would be a most

extraordinary fact if no variations had ever occurred useful to each being s own welfare in the same manner as so many variations have occurred useful to man But if variations useful to any organic being ever do occur assuredly individuals thus characterized will have the best chance of being preserved in the struggle for life and from the strong principle of inheritance these will tend to produce offspring similarly characterized This principle of preservation or the survival of the fittest I have called Natural Selection It leads to the im provement of each creature in relation to its organic and inorgan c conditions of l fe and consequently, in most cases to what must be regarded as an advance in organization Nevertheless low and simple forms will long endure if well f tted for their simple conditions of l fe

Natural selection on the principle of qualities being inherited at correspond ng ages can modify the egg seed or young as easily as the adult Amongst many animals sexual selection will have given its aid to ordinary selection by assuring to the most vigorous and best adapted males the greatest number of offspring Sexual selection will also give characters useful to the males alone in their struggles or rivalry with other males and these characters will be transmitted to one sex or to both sexes according to the form of inheritance which prevails

Whether natural selection has really thus acted in adapting the various forms of life to their several conditions and stations must be judged by the general tenor and balance of evidence given in the follow ing chapters But we have already seen how it entails extinction and how largely extinction has acted in the world s history geology plainly declares Natural selection also leads to divergence of character for the more organ c beings diverge in structure habits and constitu tion by so much the more can a large number be supported on the area of which we see proof by looking to the inhabitants of any small spot and to the productions naturalized in foreign lands There fore during the modification of the descendants of any one species and during the incessant struggle of all species to increase in number the more diversified the descendants become the better will be their chance of success in the battle for life Thus the small differences dis tinguishing varieties of the same species steadily tend to increase till they equal the greater differences between species of the same genus or even of distinct genera

We have seen that it is the common the widely-diffused and widely ranging species belonging to the larger genera within each

class, which vary most, and these tend to transmit to their modified offspring that superiority which now makes them dominant in their own countries Natural selection, as has just been remarked, leads to divergence of character and to much extinction of the less improved and intermediate forms of life On these principles, the nature of the affinities, and the generally well defined distinctions between the innumerable organic beings in each class throughout the world may be explained It is a truly wonderful fact—the wonder of which we are apt to overlook from familiarity—that all animals and all plants throughout all time and space should be related to each other in groups subordinate to groups in the manner which we everywhere behold—namely, varieties of the same species most closely related species of the same genus less closely and unequally related forming sections and sub-genera, species of distinct genera much less closely related and genera related in different degrees forming sub-families, families, orders, sub-classes and classes The several subordinate groups in any class cannot be ranked in a single file, but seem clustered round points, and these round other points, and so on in almost endless cycles If species had been independently created, no explanation would have been possible of this kind of classification, but it is explained through inheritance and the complex action of natural selection, entailing extinction and divergence of character, as we have seen illustrated in the diagram

The affinities of all the beings of the same class have sometimes been represented by a great tree I believe this simile largely speaks the truth The green and budding twigs may represent existing species, and those produced during former years may represent the long succession of extinct species At each period of growth all the growing twigs have tried to branch out on all sides, and to overtop and kill the surrounding twigs and branches, in the same manner as species and groups of species have at all times overmastered other species in the great battle for life The limbs divided into great branches and these into lesser and lesser branches, were themselves once, when the tree was young budding twigs and this connection of the former and present buds by ramifying branches may well represent the classification of all extinct and living species in groups subordinate to groups Of the many twigs which flourished when the tree was a mere bush, *only two or three, now grown into great branches, yet survive and bear* the other branches, so with the species which lived during long past geological periods very few have left living and modified descendants

From the first growth of the tree, many a limb and branch has decayed and dropped off, and these fallen branches of various sizes may represent those whole orders, families, and genera which have now no living representatives, and which are known to us only in a fossil state As we here and there see a thin straggling branch springing from a fork low down in a tree, and which by some chance has been favored and is still alive on its summit, so we occasionally see an animal like the Ornithorhynchus or Lepidosiren, which in some small degree connects by its affinities two large branches of life, and which has apparently been saved from fatal competition by having inhabited a protected station As buds give rise by growth to fresh buds, and these, if vigorous, branch out and overtop on all sides many a feebler branch so by generation I believe it has been with the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever-branching and beautiful ramifications

DIFFICULTIES AND OBJECTIONS TO NATURAL SELECTION AS SEEN BY DARWIN

Long before the reader has arrived at this part of my work, a crowd of difficulties will have occurred to him Some of them are so serious that to this day I can hardly reflect on them without being in some degree staggered but, to the best of my judgment, the greater number are only apparent, and those that are real are not, I think, fatal to the theory

These difficulties and objections may be classed under the following heads First, why, if species have descended from other species by fine gradations, do we not everywhere see innumerable, transitional forms? Why is not all nature in confusion, instead of the species being, as we see them, well defined?

Secondly, is it possible that an animal having, for instance, the structure and habits of a bat, could have been formed by the modification of some other animal with widely different habits and structure? Can we believe that natural selection could produce, on the one hand, an organ of trifling importance, such as the tail of a giraffe, which serves as a fly flapper, and, on the other hand, an organ so wonderful as the eye?

Thirdly, can instincts be acquired and modified through natural selection? What shall we say to the instinct which leads the bee to make cells, and which has practically anticipated the discoveries of profound mathematicians?

Fourthly, how can we account for species, when crossed, being sterile and producing sterile offspring, whereas, when varieties are crossed, their fertility is unimpaired?

ANSWER TO THE FIRST DIFFICULTY

On the Absence or Rarity of Transitional Varieties—As natural selection acts solely by the preservation of profitable modifications, each new form will tend in a fully stocked country to take the place of, and finally to exterminate, its own less improved parent form and other less favored forms with which it comes into competition Thus extinction and natural selection go hand in hand Hence, if we look at each species as descended from some unknown form, both the parent and all the transitional varieties will generally have been exterminated by the very process of the formation and perfection of the new form

But, as by this theory innumerable transitional forms must have existed, why do we not find them embedded in countless num' ers in the crust of the earth? It will be more convenient to discuss this question in the chapter on the Imperfection of the Geological Record, and I will here only state that I believe the answer mainly lies in the record being incomparably less perfect than is generally supposed The crust of the earth is a vast museum, but the natural collections have been imperfectly made, and only at long intervals of time

ANSWER TO THE SECOND DIFFICULTY ORGANS OF EXTREME PERFECTION AND COMPLICATION

To suppose that the eye with all its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration, could have been formed by natural selection, seems, I freely confess, absurd in the highest degree When it was first said that the sun stood still and the world turned round, the common sense of mankind declared the doctrine false, but the old saying of *Vox populi, vox Dei*, as every philosopher knows, cannot be trusted in science Reason tells me, that if numerous gradations from a simple and imperfect eye to one complex and perfect can be shown to exist, each grade being useful to its possessor, as is certainly the case, if further, the eye varies and the variations be inherited, as is likewise certainly the case, and if such variations should be useful to any animal under changing conditions of life, then the difficulty of believing

that a perfect and complex eye could be formed by natural selection though insuperable by our imagination should not be considered as subversive of the theory How a nerve comes to be sensitive to light, hardly concerns us more than how life itself originated but I may remark that as some of the lowest organisms, in which nerves cannot be detected are capable of perceiving light, it does not seem impossible that certain sensitive elements in their sarcode should become aggregated and developed into nerves, endowed with this special sensibility

In searching for the gradations through which an organ in any species has been perfected we ought to look exclusively to its lineal progenitors, but this is scarcely ever possible, and w are forced to look to other species and genera of the same group, that is to the collateral descendants from the same parent form, in order to see what gradations are possible, and for the chance of some gradations having been transmitted in an unaltered or little altered condition But the state of the same organ in distinct classes may incidentally throw light on the steps by which it has been perfected

The simplest organ which can be called an eye consists of an optic nerve, surrounded by pigment cells and covered by translucent skin, but without any lens or other refractive body We may, however, according to M Jourdain, descend even a step lower and find aggregates, of pigment-cells apparently serving as organs of vision, without any nerves and resting merely on sarcodic tissue Eyes of the above simple nature are not capable of distinct vision, and serve only to distinguish light from darkness In certain star fishes, small depressions in the layer of pigment which surrounds the nerve are filled, as described by the author just quoted, with transparent gelatinous matter projecting with a convex surface, like the cornea in the higher animals He suggests that this serves not to form an image, but only to concentrate the luminous rays and render their perception more easy In this concentration of the rays we gain the first and by far the most important step towards the formation of a true picture forming eye for we have only to place the naked extremity of the optic nerve which in some of the lower animals lies deeply buried in the body, and in some near the surface, at the right distance from the concentrating apparatus, and an image will be formed on it

In the great class of the Articulata, we may start from an optic nerve simply coated with pigment, the latter sometimes forming a sort

of pupil, but destitute of a lens or other optical contrivance With insects it is now known that the numerous facets on the cornea of their great compound eyes form true lenses, and that the cones include curiously modified nervous filaments But these organs in the Articulata are so much diversified tnat Muller formerly made three main classes with seven subdivisions, besides a fourth main class of aggregated simple eyes.

When we reflect on these facts, here given much too briefly, with respect to the wide, diversified, and graduated range of structure in the eyes of the lower animals and when we bear in mind how small the number of all living forms must be in comparison with those which have become extinct, the difficulty ceases to be very great in believing that natural selection may have converted the simple apparatus of an optic nerve, coated with pigment and invested by transparent membrane, into an optical instrument as perfect as is possessed by any member of the Articulate Class

He who will go thus far, ought not to hesitate to go one step further, if he finds on finishing this volume that large bodies of facts, otherwise inexplicable can be explained by the theory of modification through natural selection, he ought to admit that a structure even as perfect as an eagle s eye might thus be formed, although in this case he does not know the transitional states It has been objected that in order to modify the eye and still preserve it as a perfect instrument, many changes would have to be effected simultaneously, which, it is assumed, could not be done through natural selection, but as I have attempted to show in my work on the variation of domestic animals, it is not necessary to suppose that the modifications were all simultaneous, if they were extremely slight and gradual Different kinds of modification would, also, serve for the same general purpose as Mr Wallace has remarked, "if a lens has too short or too long a focus, it may be amended either by an alteration of curvature, or an alteration of density, if the curvature be irregular, and the rays do not converge to a point, then any increased regularity of curvature will be an improvement. So the contraction of the iris and the muscular movements of the eye are neither of them essential to vision, but only improvements which might have been added and perfected at any stage of the construction of the instrument." Within the highest division of the animal kingdom, namely, the Vertebrata, we can start from an eye so simple, that it consists, as in the lancelet, of a little

sack of transparent skin, furnished with a nerve and lined with pigment, but destitute of any other apparatus In fishes and reptiles as Owen has remarked, "the range of gradations of dioptric structures is very great" It is a significant fact that even in man, according to the high authority of Virchow, the beautiful crystalline lens is formed in the embryo by an accumulation of epidermic cells lying in a sack-like fold of the skin, and the vitreous body is formed from embryonic sub-cutaneous tissue To arrive however, at a just conclusion regarding the formation of the eye with all its marvellous yet not absolutely perfect characters it is indispensable that the reason should conquer the imagination, but I have felt the difficulty far too keenly to be surprised at others hesitating to extend the principle of natural selection to so startling a length

It is scarcely possible to avoid comparing the eye with a telescope We know that this instrument has been perfected by the long continued efforts of the highest human intellects, and we naturally infer that the eye has been formed by a somewhat analogous process But may not this inference be presumptuous? Have we any right to assume that the Creator works by intellectual powers like those of man? If we must compare the eye to an optical instrument, we ought in imagination to take a thick layer of transparent tissue, with spaces filled with fluid, and with a nerve sensitive to light beneath, and then suppose every part of this layer to be continually changing slowly in density, so as to separate into layers of different densities and thicknesses, placed at different distances from each other, and with the surfaces of each layer slowly changing in form Further we must suppose that there is a power, represented by natural selection or the survival of the fittest, always intently watching each slight alteration in the transparent layers and carefully preserving each which, under varied circumstances, in any way or in any degree, tends to produce a distincter image We must suppose each new state of the instrument to be multiplied by the million, each to be preserved until a better one is produced, and then the old ones to be all destroyed In living bodies, variation will cause the slight alterations, generation will multiply them almost infinitely, and natural selection will pick out with unerring skill each improvement Let this process go on for millions of years and during each year on millions of individuals of many kinds, and may we not believe that a living optical instrument might thus be formed as superior to one of glass, as the works of the Creator are to those of man?

DARWIN'S SUMMARY OF HIS ANSWER TO THE THIRD DIFFICULTY, THAT OF ACCOUNTING FOR THE ACQUISITION AND MODIFICATION OF INSTINCTS THROUGH NATURAL SELECTION

I have endeavored in this chapter briefly to show that the mental qualities of our domestic animals vary, and that the variations are inherited Still more briefly I have attempted to show that instincts vary slightly in a state of nature No one will dispute that instincts are of the highest importance to each animal Therefore there is no real difficulty, under changing conditions of life, in natural selection accumulating to any extent slight modifications of instinct which are in any way useful In many cases habit or use and disuse have probably come into play I do not pretend that the facts given in this chapter strengthen in any great degree my theory, but none of the cases of difficulty, to the best of my judgment, annihilate it On the other hand, the fact that instincts are not always absolutely perfect and are liable to mistakes that no instinct can be shown to have been produced for the good of other animals, though animals take advantage of the instincts of others that the canon in natural history, of ' Natura non facit saltum,' is applicable to instincts as well as to corporeal structure, and is plainly explicable on the foregoing views, but is otherwise inexplicable, all tend to corroborate the theory of natural selection

This theory is also strengthened by some few other facts in regard to instincts, as by that common case of closely allied, but distinct, species, when inhabiting distant parts of the world and living under considerably different conditions of life, yet often retaining nearly the same instincts For instance, we can understand, on the principle of inheritance, how it is that the thrush of tropical South America lines its nest with mud, in the same peculiar manner as does our British thrush, how it is that the Hornbills of Africa and India have the same extraordinary instinct of plastering up and imprisoning the females in a hole in a tree, with only a small hole left in the plaster through which the males feed them and their young when hatched, how it is that the male wrens (Troglodytes) of North America build "cock-nests," to roost in, like the males of our Kitty wrens, a habit wholly unlike that of any other known bird Finally, it may not be a logical deduction, but to my imagination it is far more satisfactory to look at such instincts as the young cuckoo ejecting its foster brothers, ants making slaves, the larvae of ichneumonidae feeding within the live bodies of caterpillars, not as specially endowed or created

instincts, but as small consequences of one general law leading to the advancement of all organic beings, namely, multiply, vary, let the strongest live and the weakest die

DARWIN'S SUMMARY OF HIS ANSWER TO THE DIFFICULTY AS TO THE INABILITY OF NATURAL SELECTION TO ACCOUNT FOR THE FACT THAT SPECIES WHEN CROSSED ARE STERILE OR PRODUCE STERILE OFFSPRING WHEREAS WHEN VARIETIES ARE CROSSED THEIR FERTILITY IS UNIMPAIRED

First crosses between forms, sufficiently distinct to be ranked as species, and their hybrids, are very generally, but not universally sterile The sterility is of all degrees, and is often so slight that the most careful experimentalists have arrived at diametrically opposite conclusions in ranking forms by this test The sterility is innately variable in individuals of the same species, and is eminently susceptible to the action of favorable and unfavorable conditions The degree of sterility does not strictly follow systematic affinity, but is governed by several curious and complex laws It is generally different, and sometimes widely different in reciprocal crosses between the same two species It is not always equal in degree in a first cross and in the hybrids produced from this cross

In the same manner as in grafting trees, the capacity in one species or variety to take on another, is incidental on differences, generally of an unknown nature, in their vegetative systems, so in crossing, the greater or less facility of one species to unite with another is incidental on unknown differences in their reproductive systems There is no more reason to think that species have been specially endowed with various degrees of sterility to prevent their crossing and blending in nature, than to think that trees have been specially endowed with various and somewhat analogous degrees of difficulty in being grafted together in order to prevent their inarching in our forests

The sterility of first crosses and of their hybrid progeny has not been acquired through natural selection In the case of first crosses it seems to depend on several circumstances, in some instances in chief part on the early death of the embryo In the case of hybrids it apparently depends on their whole organization having been disturbed by being compounded from two distinct forms the sterility being closely allied to that which so frequently affects pure species when exposed to new and unnatural conditions of life He who will explain these latter cases will be able to explain the sterility of hybrids This view is strongly supported by a parallelism of another kind namely, that, firstly, slight changes in the conditions of life add to the

vigor and fertility of all organic beings, and secondly, that the crossing of forms, which have been exposed to slightly different conditions of life or which have varied, favors the size, vigor and fertility of their offspring The facts given on the sterility of the illegitimate unions of dimorphic and trimorphic plants and of their illegitimate progeny, perhaps render it probable that some unknown bond in all cases connects the degree of fertility of first unions with that of their offspring The consideration of these facts on dimorphism as well as of the results of reciprocal crosses, clearly leads to the conclusion that the primary cause of the sterility of crossed species is confined to differences in their sexual elements But why in the case of distinct species, the sexual elements should so generally have become more or less modified, leading to their mutual infertility we do not know, but it seems to stand in some close relation to species having been exposed for long periods of time to nearly uniform conditions of life

It is not surprising that the difficulty in crossing any two species, and the sterility of their hybrid offspring, should in most cases correspond, even if due to distinct causes for both depend on the amount of difference between the species which are crossed Nor is it surprising that the facility of effecting a first cross, and the fertility of the hybrids thus produced, and the capacity of being grafted together—though this latter capacity evidently depends on widely different circumstances—should all run, to a certain extent, parallel with the systematic affinity of the forms subjected to experiment, for systematic affinity includes resemblances of all kinds

First crosses between forms known to be varieties, or sufficiently alike to be considered as varieties, and their mongrel offspring, are very generally, but not, as is so often stated, invariably fertile Nor is this almost universal and perfect fertility surprising when it is remembered how liable we are to argue in a circle with respect to varieties in a state of nature and when we remember that the greater number of varieties have been produced under domestication by the selection of mere external differences, and that they have not been long exposed to uniform conditions of life It should also be especially kept in mind that long-continued domestication tends to eliminate sterility, and is therefore little likely to induce this same quality Independently of the question of fertility, in all other respects there is the closest general resemblance between hybrids and mongrels, in their variability, in their power of absorbing each other by repeated crosses and in their inheritance of characters from both parent forms.

Finally, then, although we are as ignorant of the precise cause of the sterility of first crosses and of hybrids as we are why animals and plants removed from their natural conditions become sterile, yet the facts given in this chapter do not seem to me opposed to the belief that species aboriginally existed as varieties.

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GLOSSARY

Acquired character —Any change in the body (soma) of an individual due to change of function or change of environment Same as Modification

Adaptation —Any character structural or functional in an organism that helps to enhance the fitness of that organism

Agamic reproduction —*See* Asexual reproduction

Allelomorph —One of a pair of contrasted characters one of a pair of genes (factors) determining the development of such characters and believed to occupy equivalent loci in homologous chromosomes a Mendelian pair

Analogous structures —Any two or more structures that subserve the same function in the different kinds of animals or plants but which arise from different embryonic rudiments and have fundamentally different structural constitutions Contrast with Homologous structures

Anthropoid —Literally manlike refers especially to the manlike apes

Apogamy —A term used by botanists synonymous with Parthenogenesis.

Asexual reproduction —Any method of reproduction that does not involve the union of gametes (Some authorities consider parthenogenesis as a phase of asexual reproduction)

Atavism —The cropping out of ancestral characters in an individual

Atrophy —The dwindling away of a structure in an individual or in a race

Autosome —Any chromosome other than those that are recognized as especially involved in the heredity of sex See Sex chromosome

Biometry —That branch of biology that investigates organic differences by statistical methods.

Blastula —An early embryonic stage consisting typically of a hollow ball of cells

Castration —The removal from an organism of the gonads (testes or ovaries)

Catastrophism —The idea held by Cuvier and others that the geologic strata were sharply marked off from one another because great catastrophies had brought each era to an end and that all life was destroyed in each catastrophe Contrast with Uniformitarianism

Cell —The smallest unit of living substance that can exist in a free state the unit out of which tissues are composed

Centrosome —An organ of a cell which seems to be a center of forces that express themselves in mitotic cell division

Character —One of many structural or functional details that characterize an individual or a race

Chromatin —The substance of which chromosomes are largely composed, the chemical composition of which is not exactly known, supposed to be *the* hereditary substance, so called because it stains readily with certain dyes and can be easily seen under the microscope

Chromosomes —The definite masses of chromatin that have a characteristic number, size and shape in any given species

Combinations —New organic conditions due to a new assortment of old factors already present in the germ plasm of parents

Commensalism.—The habitual living together of two or more different species of animals or plants involving more or less interdependence

Crossing-over —Exchange of genes (factors) between homologous chromosomes, believed to occur during synapsis

Cytology —The detailed microscopic study of the structure of cells especially of germ cells

Cytoplasm —All of the living material of the cell outside of the nucleus

Determiner —*See* Gene *or* Factor

Dihybrid cross —A crossing of two parents differing from each other in only two pairs of allelomorphs

Diploid —The maximum or full (duplex) number of chromosomes found in body cells and in the unmaturated germ cells twice the gametic or haploid number

Dominant.—A term applied to that member of an allelomorphic pair of characters that has the capacity of manifesting an effect wholly or partly to the exclusion of the effect of the other member (the recessive)

Duplicate factors (genes) —*Two or more factors located in different* chromosomes, either of which produces the same result

Egg —The female germ cell more precisely the female gamete

Environment.—The sum of all influences upon the organism that have their origin outside of the body

Epigenesis —The doctrine that the germ cell is absolutely or relatively structureless and that differentiation arises *de novo* through the interaction of the protoplasm and the environment Contrast with Preformation

F_1 generation —The first hybrid generation of a hybrid cross exhibits only the dominant characters of the two parents

F_2 generation —The offspring resulting from the interbreeding of individuals of the F_1 generation

F_3 generation —The offspring resulting from the interbreeding of individuals of the F_2 generation

Factor —A unit of inheritance situated at some particular locus of a particular chromosome and transmitted according to the laws of Mendel a determiner or gene

Faunas —Groups of animals inhabiting a given geographic region or geologic period

Fertilization.—The union of male and female gametes and the consequent initiation of development of a new individual.

Floras.—Groups of plants inhabiting a given geographic region or geologic period

Gamete.—A mature male or female reproductive cell, containing the haploid number of chromosomes, an egg or a spermatozoön

Gametic Reproduction.—*See* Sexual reproduction.

Gastrula.—A stage in the development of metazoan animals in which the embryo consists of two germ layers, ectoderm and endoderm.

Gemmules.—Hypothetical inheritance units involved in Darwin's provisional theory of pangenesis

Gene.—*See* Factor

Genetics.—The science which seeks to explain the resemblances and differences in organism related by descent, the modern analytic and experimental study of variation heredity, and sex

Genotype.—A group of individuals all of which are alike in their genes or factors. Contrast with Phenotype

Genotypic.—Pertaining to the germinal or hereditary constitution of an organism. Contrast with Phenotypic

Genus.—An arbitrary group in the systematic classification of animals or plants, ranking above the species and containing one or more species possessing structural characters differing from those of other genera

Germ cell.—A cell specialized for sexual reproduction. Matured germ cells are known as gametes

Germ plasm.—That part of the cell protoplasm which is believed to be the material basis of heredity and is transferred from one generation to the next. Contrast with Somotoplasm or Soma

Germinal continuity.—The concept of an unbroken stream of germ plasm from generation to generation back to the beginning of life

Gonads.—The organs (ovaries or testes) that contain the reproductive cells or germ cells and sometimes also contain glandular tissue that functions in the differentiation of secondary sexual characters.

Gynandromorph.—An animal in which one part exhibits male characters and another part female characters.

Habitat.—The complex of environmental factors making up the surroundings of any species or race

Haploid.—The reduced (one-half) number of chromosomes present only in gametes *See* Diploid

Hermaphrodite.—An individual organism possessing both ovaries and testes.

Heterogenesis.—*See* Mutation

Heterozygote.—An individual or a zygote resulting from the union of unlike gametes.

Heterozygous.—Having the allelomorphic pairs composed of dissimilar elements, resulting in the production of more than one kind of gametes

Heterozygous sex.—The sex in which the members of the chromosome pair that determines sex are unlike

Homologous structures.—Any two structures either in the same or in different individuals or species that arise from equivalent embryonic rudiments and have the same structural relations to other parts irrespective of the function subserved Contrast with Analogous structures

Homozygote.—An individual or a zygote resulting from the union of like gametes

Homozygous.—Having the allelomorphic pairs composed of similar elements, resulting in the production of only one kind of gamete

Homozygous sex.—The sex in which the members of the chromosome pair that determines sex are alike

Hormone.—A substance secreted by one of the endocrine glands, that affects the development of or the functioning of some other part or parts of the body

Indigenous.—Living naturally in any country or climate Contrast with Introduced

Induction.—Any change in a germ cell or an embryo that persists for only a few generations and then disappears Contrast with Mutation

Introduced.—Brought in from another country and living more or less successfully under foreign conditions Contrast with Indigenous

Isolation.—The process of separating one section or strain of a species from another section or from the main body of the species believed to facilitate the establishment of new species

Lamarckian.—Pertaining to Lamarck's doctrine of the inheritance of acquired characters

Lamarckism.—The theory of the inheritance of acquired characters

Larva.—A self supporting embryo, a developmental stage of an animal in which various adaptive structures for self support appear that may or may not be significant for the development of adult structures

Lethal.—Producing death, destructive of life

Linin.—An achromatic or non-chromatin substance that forms a net work of threads in the nucleus

Linkage.—The type of inheritance in which genes (factors) tend to remain together in transmission from generation to generation owing to their location in the same chromosome

Locus (*pl* loci).—A definite point or region in a given chromosome at which is located a genetic factor or gene

Maturated germ cell.—*See* Gamete

Maturation.—The process through which germ cells pass in preparation for fertilization usually resulting in the formation of gametes

Mitosis.—The normal process of cell division involving the formation

of spindle, chromosomes, etc , and resulting in longitudinal splitting of each chromosome

Modification.—A change in the body or soma of an individual due to functioning or to use and disuse, same as Acquired character

Monohybrid cross —A cross between two individuals differing in only one pair of allelomorphs

Morphological —Structural, opposed to physiological

Multiple allelomorphs —Different factors or genes occupying the same locus of homologous chromosomes, the character conditioned by such factors

Multiple factors —Two or more factors usually alike in character, which unite in various numbers to produce different quantitative expressions of one character Same as Duplicate factors

Mutant.—An individual having a different genotypic constitution from its parents, as the result of a change in the germ plasm, and not as the result of segregation or crossing-over Some authorities include the type of changes due to chromosomal aberrations under the head of mutants while others limit mutants to those resulting from factor changes

Mutation —The germinal change resulting in the production of a mutant The definition of mutation differs according to differences of opinion as to what should be included under the definition of a mutant Contrast with Induction

Neo-Darwinian —A descriptive term applied to theories based on Darwin's theory of natural selection.

Neo-Lamarckian —A descriptive term applied to theories based on Lamarck's theory of the inheritance of acquired characters

Neo-mutationist —A modern adherent of the mutation theory, especially one who is interested chiefly in tracing the origin of germinal changes that are responsible for the appearance of mutants

Non-disjunction.—The failure of the two members of a pair of homologous chromosomes to separate in cell division, with the result that they both pass into one daughter-cell, making one too many chromosomes in one gamete and one too few in the other

Nucleus —The body within a cell that contains the chromatin

Ontogenetic —Pertaining to the life history of the individual Contrast with Phylogenetic.

Ontogeny —The developmental history of the individual, same as development or somatogenesis Contrast with Phylogeny

Orthogenesis —The apparent fact that races or groups of animals or plants vary progressively along definite lines, each variation forming the threshold of departure for the next and the whole series forming a definite sequence, definitely directed evolution

Ovule —The body that contains the egg of flowering plants and becomes the seed after fertilization and maturation.

Ovum (*pl* ova) —The egg, the type of gamete produced by a female

Pangenesis.—A provisional theory as to the mechanism of hereditary

transmission devised by Charles Darwin It implies the idea that the germ cells are made up through the process of collecting from the blood stream gemmules or representatives of all parts of the body In this way each structure of the adult parent would be present in the germ cell and would be transmitted to the offspring

Panmixia.—An early theory of Weismann designed to account for the rudimentation of structures almost equivalent to cessation of natural selection

Parthenogenesis.—The development of an egg without fertilization A process in animals equivalent to Apogamy in plants

Peculiar —A term used technically to describe a species or higher group of organisms occurring in one region and nowhere else

Pedigree —An ancestral history a genealogical tree

Phenotype —A group of individuals which are alike somatically and look alike but which may differ germinally the sum of the visible features of an individual or a race Contrast with Genotype

Phenotypic.—Pertaining to the somatic appearance of the individual or group of individuals. Contrast with Genotypic

Phylogenetic —Pertaining to the ancestral history of a group Contrast with Ontogenetic.

Phylogeny —The history of the evolution of a species or a group as distinguished from Ontogeny

Preformation —A theory that the individual is preformed in the egg and needs only to grow or to unfold in order to reach its definitive state Contrast with Epigenesis

Protoplasm —The living substance of cells

Pure line —The descendants of a single individual that have not undergone any germinal change

Quadrumana —An old name for apes and monkeys implying that their hands and feet are both grasping appendages like hands

Recessive —The opposite of dominant

Segregation.—The separation into separate gametes of the two members of a pair of allelomorphs resulting in gametes pure for one or the other of a pair of allelomorphic genes

Serology —That branch of experimental biology or medicine that deals with the reactions of the blood to foreign materials and the production of antibodies the science of serums.

Sex chromosome —The particular chromosome (the X-chromosome for example) that seems to carry the factors for sex and through which sex is inherited.

Sex linked.—A term applied to characters located in the sex chromosomes.

Sex ratio.—The relative proportion of the two sexes in a population.

Sexual reproduction —That mode of reproduction that involves the union of gametes to form a zygote Same as Gametic reproduction.

Simian —Pertaining to apes

Soma.—The body of an organism as contrasted with the germ cells

Somatic —Pertaining to the body Contrast with Germinal

Somatoplasm —Same as Soma Contrast with Germ plasm

Special creation —A popular doctrine holding that all species existing today were created by divine fiat within a few days and that they have not materially changed

Species —A group of varieties or a single variety which, in botanical or zoölogical characters and genetic relationship, can be differentiated from all other groups or varieties

Sperm —A short term for the male gamete

Spermatozoön —The longer technical term for the functional male gamete

Sporadic —Occurring singly, scatteringly, or apart from others of the same kind

Symbiosis —*See* Commensalism

Systematist.—A taxonomist or specialist in the science of classification

Synapsis —The pairing off and lying together of homologous chromosomes, prior to the maturation division

Taxonomy —The science of classification

Teleology —The doctrine that the processes of nature were originally purposed or planned the doctrine of design

Tetraploidy —That chromosomal condition where the germ cells in some way acquire four times the haploid number of chromosomes, thus some so-called plant mutants are tetraploid

Trihybrid cross —A hybridization experiment in which the parents differ with regard to three pairs of allelomorphs

Triploidy —That chromosomal condition where the germ cells in some way acquire three times the haploid number of chromosomes, some so called plant mutants are triploid

Uniformitarianism —The theory that the changes of the past may be interpreted in terms of the changes of the present and that most changes are of a slow gradual kind Contrast with Catastrophism

Variety —A group of individuals within a species which resemble one another but differ in some respects from other members of the species

X-chromosome —The so-called sex chromosome

Y-chromosome —The chromosome that usually pairs off with the X-chromosome in synapsis It does not seem to carry any genetic factors except possibly that of fertility

Zygote —A combination germ cell formed by the fusion of two gametes the individual, with the diploid number of chromosomes that result from the development of a fertilized egg

Zygotically —Pertaining to the zygote or fertilized egg

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